GROWTH OF INTERIOR SPRUCE AND ATTACK BY THE WHITE PINE WEEVIL, *PISSODES STROBI* (PECK) IN THE SUB BOREAL SPRUCE ZONE OF BRITISH COLUMBIA: ROLE OF OVERSTOREY SHADE

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Susan M. Nykoluk

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Name: Susan M. Nykoluk

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Examining Committee:

Chair: Dr. Karin Beeler
Associate Professor, English Program
UNBC

Supervisor: Dr. Chris Hawkins
Associate Professor & Endowed Chair, Forestry Program
UNBC

Committee Member: Dr. Russell Dawson
Assistant Professor, Biology Program
UNBC

Committee Member: Dr. René I. Alfaro
Senior Scientist
Canadian Forest Service

Committee Member: Dr. Jian Wang
Assistant Professor, Faculty of Forestry & the Forest Environment
Lakehead University

External Examiner: Dr. John H. Borden
Professor, Department of Biological Sciences
Simon Fraser University

Date Approved: 26 FEB 02

ABSTRACT

A portion of an interior spruce plantation, planted in 1989, in the SBSvk1 was aerially-sprayed with the herbicide glyphosate in 1996, while the remaining area was left untreated. The untreated area has an overstorey of paper birch, *Betula papyrifera* Marsh.. The plantation, 100 km east of Prince George, was surveyed for attack by the white pine weevil, *Pissodes strobi* (Peck), and tree growth was measured. Attack rates on spruce were markedly lower in the untreated, or control, portion of the plantation compared to the herbicide treated area for 2000 and 2001. Mean spruce, *Picea glauca* (Moench) Voss x *Picea engelmannii* Parry ex Engelm, height was 0.85 m greater in the control compared to the treated area in 2001. There was no difference in diameter at breast height. Spruce trees growing with birch had better form than trees growing in the open. Paper birch at a maximum of 3500 stems per hectare (sph) did not impede the growth of spruce.

Two experiments were established with interior spruce seedlings, and artificial shade to determine effects of light on the behaviour of weevils. In five open pollinated families of spruce in 2000, weevils oviposited lower on the terminal leader on trees under shade. However, overall attack success was unrelated to shade treatment or ranking of resistance. During 2001, older propagules (emblings) produced by somatic embryogenesis (SE) were used. Overall success of attack was unrelated to shade, and there was no relationship between total number of oviposition punctures and shade treatment. Shade level may have affected oviposition behaviour but the spectral properties of artificial and natural shade are different and may influence the behaviour of weevils. Resistance to attack by weevils in unshaded SE clones followed original resistance rankings of the parent trees.

Findings suggest that overstorey shade created by birch reduces attack by weevils on spruce, without reducing the rate of growth or form of interior spruce. Further studies are needed to determine whether this relationship is specific to paper birch, or generalized to all broadleaf species.

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CHAPTER 1

Introduction and Review of the Literature

1.1 Introduction

The white pine weevil, *Pissodes strobi* (Peck) (Coleoptera: Curculionidae), is a serious pest of many young spruce plantations in the British Columbia because it destroys the terminal shoot of young spruce trees causing stem defects and reducing height growth (Silver 1968; Alfaro 1982). The Sub Boreal Spruce (SBS) and Interior Cedar Hemlock (ICH) Bigeoclimatic zones (Meidinger *et al.* 1991) are considered to be high hazard zones for weevil infestation with an estimated 400,000 ha at risk in the central British Columbia interior based on degree-day requirements for larval development (Spittlehouse *et al.* 1994). The SBS and ICH are characterized by long cold winters and relatively warm moist, but short summers (Meidinger *et al.* 1991; Coates *et al.* 1994). The weevil is thought to be the most destructive pest of second-growth spruce in British Columbia (Alfaro and Borden 1985). At present, after regeneration, licensees have the legal obligation of ensuring their plantations reach a free-growing status within an allotted time period (BC Ministry of Forests 2000). These recommendations may however, have negative effects regarding rates of weevil-infestation and recovery of spruce after attack. Species of deciduous-brush are removed from plantations to allow crop trees to grow without competition. In doing so, favourable conditions are created for weevil infestations due to increased light and temperature (Lanier 1983; Alfaro *et al.* 1994; Alfaro 1998).

Historically, weevil infestations have been of concern mainly in coastal British Columbia on Sitka spruce, *Picea sitchensis* (Bong) Carr.[1] This is largely due to the activity of reforestation occurring in this region. However, recent evidence has shown that white pine weevil may become

[1] All tree names and authorities taken from: Farrar, J.L. 1995. Trees in Canada. Fitzhenry & Whiteside Ltd. and the Canadian Forest Service. 501pp.

just as damaging in the interior of BC as much of the region has been replanted over the past 20 years (Alfaro 1998). It is difficult to determine the total area at risk to weevil infestation. Previously, estimates of 34,000 ha were said to be at risk in the Prince George Forest District in 1994, with an additional 100,000 hectares reaching susceptible levels within the following decade (Hall 1994). Hazard levels are based upon biogeoclimatic subzones and elevations, which allow for the required degree-days needed for insect development from larva to adult (Spittlehouse *et al.* 1994; Taylor 1997). Temperatures relating to these subzones are generally recorded from airport weather stations and are somewhat limited in their scope in that they cannot accurately represent the variety of microclimatic conditions that occur in a forest or stand (McIntosh 1997).

Previous studies (Cozens 1983; McLean 1994; Taylor *et al.* 1996) have shown that a deciduous overstorey reduces attack by weevil on spruce. In addition, shade from deciduous overstorey may positively affect the post-attack recovery of interior spruce trees by allowing the terminal shoot or a lateral to take over and resume a normal growth pattern and apical dominance much sooner than in the open. Return to a normal pattern of development allows trees to resume growth at more predictable rates, reducing losses in height. This ultimately translates into greater gains in volume and wood quality than would be the case with slow recovery in the open. There has been much evidence showing that conifers grown with deciduous species show greater resistance to attack by weevil (Stiell and Berry 1985; McLean 1994; Taylor and Cozens 1994).

Past research focused on the role of physical factors such as temperature (Sullivan 1959; Sullivan 1960; McMullen 1976), and light (Sullivan 1961; VanderSar and Borden 1977) to explain why overstorey mitigates attack by weevil. These and many other factors, may interact to reduce attack by weevils under shaded conditions. This thesis investigates some of these factors to help determine the mechanism by which attacks by the white pine weevil, at both the tree- and stand-level on interior spruce, *Picea glauca* (Moench) Voss x *Picea engelmannii* Parry ex Engelm., are reduced under shade.

1.2 Taxonomy and Life Cycle of *Pissodes strobi*

The white pine weevil was first recognized as a destructive pest of the dominant shoot of the Weymouth pine (eastern white pine), *Pinus strobus* L. in 1817 by W.D. Peck, Professor of Natural History and Botany at Harvard University (Belyea and Sullivan 1956). Hopkins (1907, 1911), who first described a detailed life history of this insect, originally recognized 30 North American species in the genus *Pissodes*. The genus *Pissodes* (Langor 1998) now contains 29 described species in North and Central America, all of which are associated with conifers. *P. strobi* is considered to be the most damaging of the genus *Pissodes*, but other insects within it include: *P. terminalis* Hopping, the lodgepole pine terminal weevil, *P. nemorensis* germar, *P. schwarzi* Hopkins, which attack the boles of weak and dead trees and *P. fasciatus LeConte* which has been suspected in the spread of fungal diseases of conifers (Langor 1998).

Classification of *Pissodes strobi* was originally based upon insect morphology and the association with host-trees. In British Columbia, species were previously called *Pissodes sitchensis* Hopkins, *Pissodes engelmanii* Hopkins, and *Pissodes strobi* (Peck) in accordance with the insect's locale and host tree (Hopkins 1911; Manna and Smith 1959). Later this evidence was refuted through breeding experiments (Manna and Smith 1959; Smith 1962; Smith and Sudgen 1969), physiological evidence (VanderSar *et al.* 1977) and protein electrophoresis (Phillips and Lanier 1985). Thus, all three populations were considered to be of the same species. More recently, randomly amplified polymorphic DNA (RAPD) marker studies have indicated three separate genetic subspecies of *P. strobi* in British Columbia and one subspecies east of the Rocky Mountains (Lewis 1995; Lewis *et al.* 2000). Although evolutionary divergence has occurred between populations, all subspecies are currently known by the binomial, *Pissodes strobi* (Peck).

Pissodes strobi produces one generation per year and has a maximum life span of four years (McMullen and Condrashoff 1973; Kline and Mitchell 1979; Wood and McMullen 1983). Adults emerge from hibernation in the spring when snow has melted from the base of trees, and the forest floor where they overwinter has warmed to 6°C or greater (Sullivan 1959). Adults then move

up the stem of the host tree to begin feeding on shoots (Sullivan 1960). Stevenson (1967) observed that feeding by weevils occurred on the uppermost portions of stems on the north side of dominant leaders. Weevils are diecious and mating generally occurs on the tree's terminal shoot (Hopkins 1911). It is possible that pheromones play a role in attracting weevils during breeding; however, no pheromone has been definitively identified (Booth and Lanier 1974; Phillips and Lanier 1986). Egg laying, or oviposition, by females occurs under or in the bud of the terminal branch from the previous year. Frequency and distribution of eggs has been shown to be affected by shade for insects feeding on white pine (Sullivan 1961). Eggs are laid in feeding punctures, occasionally in groups of two or three (Gara *et al.* 1971) but are usually single. As many as five eggs have been reported in a single puncture (McMullen and Condrashoff 1973). In a single leader, as many as 200 eggs may be laid (Wallace and Sullivan 1985) although a mean of 64 eggs are laid in Sitka spruce (Silver 1968). Females tend to lay all their eggs in a single leader (Stevenson 1967; Silver 1968). The fecundity of weevils remains constant throughout their life span (Stevenson 1967; Gara *et al.* 1971; McMullen and Condrashoff 1973). This was confirmed by Trudel and Lavallée (2001) who showed that two-year old females produced as many eggs and oviposited at the same rate, on white pine, as did one-year old weevils. Eggs of *P. strobi* are oval, white-opalescent and measure 1.0 mm by 0.5 mm (Wood and McMullen 1983; Turnquist and Alfaro 1996). After the eggs are laid, they are covered with a dark-coloured fecal plug. Gara *et al.* (1980) hypothesized that the fecal plug served the purposes of identification of an egg-containing cavity to other weevils and protection against egg predation by other species.

Larvae begin feeding as soon as they hatch, which occurs approximately two weeks after the eggs are laid (Belyea and Sullivan 1956). They feed in a ring and move downwards as a group while feeding on the phloem tissue. Larvae feed for about five to six weeks, by which time infested leaders are killed (Belyea and Sullivan 1956). The new terminal shoot of the tree eventually turns a yellow-redish colour and starts to droop because the downward feeding of the larvae on the phloem gradually severs the xylem tissue (Mitchel *et al.* 1990). The tree's needles turn red in late summer

or early fall and eventually fall off in subsequent years. The larvae go through four instars, which are identified by the size of the head capsule (Silver 1968). Development for an individual larva to the pupal stage takes about 34 days, although there is much variation in dates between oviposition and hatching for individual larvae (Stevenson 1967). In mid-summer, larvae form pupal chambers or chip-cocoons out of xylem fibres. In stems less than 1.9 cm in diameter the larvae almost always pupate in the pith without chip-cocoons (Stevenson 1967). Pupation takes approximately two weeks after which the new adults emerge or stay within the stem for another two weeks (MacAloney 1930). Adults emerge in late summer or early fall after chewing holes through the bark (Stevenson 1967). There is generally one emergence hole per weevil (Nealis 1998). Adult weevils are approximately 0.5 cm long with a long curved snout and cylindrical body. The elytra contain patches of light brown or grey scales (Belyea and Sullivan 1956).

Weevils emerging in the fall tend not to fly due to flight muscles being undeveloped compared to spring adults (Stevenson 1967). Stevenson (1967) showed this using 136 newly emerged fall adults. After subjecting half to a cold treatment of 2.22°C (36°F) and the other half to warmer temperatures (18.33°C-22.22°C, 65-72°F) for 48 days he tested their flight response. Only weevils that had been subjected to cold temperatures were capable of flight. Dissections revealed undeveloped flight muscles in individuals that had not been subjected to cold treatment (Stevenson 1967). Belyea and Sullivan (1956) noted that adult weevils emerging in the fall do not mate and oviposit at this time but are limited to feeding on branches. When temperatures drop below 5°C weevils move to the duff layer of the forest floor, usually under the tree from which they emerged, and find hibernation sites (Sullivan 1959). In the Prince George region, this usually occurs in late September or early October (Cozens 1983).

1.3 Distribution of *P. strobi* and Host Trees

Pissodes strobi is native to North America and ranges from the Pacific to Atlantic coast, as far north as 60°N in the Yukon and Great Slave Lake in the Northwest Territories (Brown *et al.*

1960), and as far south as central Colorado in the west and northern Georgia in the east (Hopkins 1911; Humble *et al.* 1994; Langor and Sperling 1995). In the east, *P. strobi* has mainly been found in the Southern boreal forest of Ontario, Quebec and the Maritime provinces of New Brunswick, Nova Scotia and Prince Edward Island (Humble *et al.* 1994). VanderSar *et al.* (1977) showed that *P. strobi* from the Pacific Coast fed on white pine as readily, as on spruce, but *P. Strobi* from the East did not feed on spruce from the west. From this he concluded that *P. strobi* probably originated in the East (VanderSar *et al.* 1977).

In eastern Canada, the weevil is a pest primarily to eastern white pine, *Pinus strobus* L. and the exotic Norway spruce, *Picea abies* (L.) Karst., while in the west it primarily attacks Sitka, *Picea sitchensis* (Bong) Carr., white, *Picea glauca* (Moench) Voss, Engelmann Spruce, *Picea engelmanii* Parry, and interior spruce, *Picea glauca* (Moench) Voss x *Picea engelmannii* Parry ex Engelm (Belyea and Sullivan 1956). Pines are the primary hosts in the Maritime Provinces. There are several other North American trees that are also attacked by *P. strobi* but usually not at epidemic levels (Humble *et al.* 1994). The following species of spruce have also been shown to host the weevil: black spruce, *Picea mariana* (Mill.) B.S.P., Parry, red spruce, *P. rubens* Sarg, and Colorado spruce, *P. pungens* Engelm. (Humble *et al.* 1994). Other pines which have been shown to host the weevil include jack pine, *Pinus banksiana* Lamb., lodgepole pine, *Pinus contorta* Dougl. Ex Loud. var. *latifolia* Engelm., red pine, *P. resinosa* Ait., Austrian pine, *P. nigra* Arn., and two exotic pine species: Mugho pine, *P. mugo* Turra, and Scots pine, *P. sylvestris* L. (Humble *et al.* 1994).

Epidemic levels, greater than 20% of trees attacked by weevils in a single year, on Sitka spruce in some coastal regions has led to shifting planting preferences to entirely different species (Wallace and Sullivan 1985). The only coastal region of British Columbia that has been unaffected by the weevil so far, is the Queen Charlotte Islands, where the insect has never been reported (Humble *et al.* 1994; Turnquist and Alfaro 1996).

1.4 Control Methods - Past and Present

Many methods have been used in an attempt to control the weevil and lessen the damage and financial losses incurred by *P. strobi*. Some of these methods were costly, while others were potentially detrimental to the environment. A brief summary of these methods follows.

1.4.1 Mechanical Control

Mechanical control of weevils by clipping attacked leaders before adult emergence has been tried but has largely proven to be costly and ineffective in BC. Peck first recommended this mode of control in 1817 (Belyea and Sullivan 1956). Before chemical insecticides were used, leaders were clipped and burned (de Groot and Helson 1994). Heppner (1989) conducted a clipping trial on Sitka spruce, which was partly successful. McLean (1989) found high numbers of predators in leaders and noted that leader clipping removes the beneficial insects, which overwinter in the leaders. Rankin and Lewis (1994) calculated that the mean cost for clipping was $250/ha. They placed infested leaders in screened pails to allow for the escape of predators and parasites but to keep adult weevils inside. Although leader-clipping proved to be successful in reducing damage it is not economically feasible on a large operational scale.

1.4.2 Chemical Control

A complete historical description on the use of chemical control to fight weevil outbreaks since 1886 is given by de Groot and Helson (1994). At the turn of the century, copper aceto-arsenite wash, known as "Paris Green" was applied to susceptible trees. Since then, other chemicals including soap mixed with Paris Green, lime sulphur, shale oil soap, sulphur, lead arsenate and kerosene have been tried. During the 1920's and 1930's silvicultural practices began to overshadow chemical control but by the 1950's, after successful field trials of DDT, dichlorodiphenyltrichloroethane, it was thought that a solution to weevil outbreaks had been found. Aerial control trials with DDT were first undertaken in Ontario 1957 and again from 1961 to 1973.

Use of insecticides peaked from the mid-1960's to early 1970's. Some of these included malathion, carbaryl, Zectran, Bidrin, heptachlor, dimethoate, Metasystox-R, Guthion, endosulfan, and dieldrin (de Groot and Helson 1994). In the early 1970's, concern for the impact of insecticides on the environment became more prominent. Many of the above-listed chemicals have since been banned for use in North America. Systemic spray applications have also been tested in ground spraying trials as well as soil applications aimed at overwintering populations (de Groot and Helson 1994). Bradbury (1986) also applied Metasystox-R to determine if it had any effect on larvae inside the leader. He found that four applications at 10-day intervals offered complete protection of the leader. Fraser and Heppner (1993) also reported that stem implants with acephate were effective in controlling weevils on Sitka spruce.

Due to the many constraints of using insecticides it was concluded that chemical application was best used in high-value plantations where other management practices are impractical or inadequate. Currently, insecticides for controlling attacks by weevil are considered inappropriate in moderate to large plantations due to potential damaging environmental effects (de Groot and Helson 1994).

1.4.3 Biological Control, using Natural Enemies

Although there have been relatively few studies on biological control of weevils, previous studies (Stevenson 1967; Hulme *et al.* 1987; Hulme and Harris 1988) have shown that many parasites and predators associated with *Pissodes strobi* may be effective for population control. Nealis (1998) stated that the relationship among predators and parasitoids, may be as much of a factor in rates of attack as physical and biotic changes associated with the growth of host trees. Most natural enemies are either dipteran predators, or hymenopteran parasitoids. In a study of weevil populations in jack pine in Ontario, there was a strong negative relationship with the dipteran parasite *Lonchaea corticis* Taylor and weevil emergence (Nealis 1998). Without natural enemies, weevil populations could be as much as three times greater (Nealis 1998). Stevenson

(1967) found that *L. corticis* destroyed about 20% of the larvae and pupae in his study. Predation by birds may contribute to reducing populations of weevils (Taylor 1929; Bellocq and Smith 1994), although rates of predation may vary depending on the overstorey species (Taylor 1997) and the abundance of weevils (Nealis 1998).

Hulme (1994) thought that the braconid wasp, *Allodorus crassigaster* Provancher, was a potential insect to use for biological control of the weevil because of its ability to kill a large proportion of the brood of weevil larvae. Female wasps lay their eggs in the eggs of weevils by inserting their oviopositor through the fecal cap left after egg laying by the weevil. The larvae of the wasp then develop to the first instar inside the weevil egg capsule. When the weevil-larva begins to pupate the larva of the wasp molts to the second instar and begins to feed on the weevil larva from the inside (Hulme 1994). At this time, biological control of the weevil is not used as a management practice.

1.4.4 Genetic Resistance

Genetic resistance of a tree to attack by white pine weevil is varied as it often involves the combination of several traits. Because the genetics of *P. strobi* vary by population and by region, what may act as a resistance mechanism in one genotype of spruce may not act as a resistance mechanism in another. Combined with the interactions of differences in site, changing climate, and fluctuating populations, determining genetic resistance of a species of tree is sometimes difficult. The processes that lie beneath particular defence mechanisms may not be active all the time, but may be triggered in the spring by environmental factors (Alfaro 1997). The favoured host individuals of *P. strobi* are the most rapidly growing sapling and pole-sized trees of either spruce or pine in the stand (Lanier 1983). King *et al.* (1997) showed that weevils preferred fast growing interior spruce trees as hosts, but also showed that fast growing families had high levels of genetic resistance to attack. Hulme (1995) observed that the least-damaged trees in a Sitka spruce provenance started development of apical buds earlier than did susceptible clones. He also showed

that when the phenology of the clones was delayed, weevils would attack the resistant genotypes. Subsequently, Alfaro *et al.* (2000) showed that early development of buds in Sitka spruce is sometimes weakly correlated with resistance to weevils.

Genetic variation among families of spruce with regard to rate of attack and damage has been found in interior and Sitka spruce (Alfaro 1997). Trees have been regarded as tolerant to attack if they have the ability to recover from weevil damage (Alfaro and Ying 1990), but are regarded as resistant to attack if they have the ability to avoid, or fend off, attacks (Mitchel *et al.* 1990; Kiss and Yanchuk 1991). Variation in genetic resistance has been shown within families of spruce (Alfaro *et al.* 1996a). In white spruce, the resistant families are typically the fastest growing trees (Alfaro *et al.* 1996a; King *et al.* 1997). Ying (1990) found resistance in at least three provenances of Sitka spruce in coastal British Columbia. Within these families he found 15 times less attack on the resistant families compared to the most susceptible families (Ying 1990).

Resistance to weevil may be due to a combination of mechanisms. For example, Tomlin and Borden (1997a) and Tomlin *et al.* (1996) showed resin ducts, which contain terpenes and high amounts of cortical resin acid are important in resistance to weevil. Resin is considered to be a defensive mechanism of conifers that deters attack, prevents fungal growth and drowns eggs and larvae (Berryman 1972). Tomlin *et al.* (1996) found Sitka spruce trees with very high levels of acid in the resin may have a greater capacity to deter feeding or produce resin which is toxic to eggs and larvae. In addition, foliar terpenes have also been shown as a mechanism of resistance to weevils in Sitka spruce (Tomlin *et al.* 1997). Nault *et al.* (1999) found that levels of terpenes or other volatiles in the leaf or bark of white and Engelmann spruce were highly correlated within ramets of highly variable progeny and concluded that the level of terpenes is not a useful tool for selecting resistant genotypes.

Alfaro (1995) showed that an induced defence reaction occurred in Sitka spruce after weevils began feeding and laying eggs. The reaction consisted of the cambium cells switching from producing normal tracheids and parenchyma cells, to producing traumatic resin canals that killed

eggs and larvae (Alfaro 1995). Tomlin and Borden (1998) found Sitka spruce trees from families with know resistance responded with faster and with greater intensity than trees from susceptible families in producing traumatic resin canals. Sahota *et al.* (1994) proposed that chemicals in the bark of resistant spruce could hamper reproduction in female weevils by causing ovarian regression or inhibition of development.

Although genetic resistance found in host species shows promise, resistance as a control mechanism may be impeded by the insect's ability to adapt. Alfaro (1996) found that females confined to resistant trees oviposited lower in the stem, below the leader, where resin canal density was reduced due to increased stem diameter, thereby preventing the brood from being drowned. Use of resistant stock, such as that produced by somatic embryogenesis technology, promises to be a valuable tool for pest management but will need to be used with other control methods, such as silviculture, to minimize the effects of adaptation by the weevil. Alfaro *et al.* (1995) suggested a system of integrated pest management, which incorporates hazard assessment with the planting of genetically resistant stock.

1.4.5 Silviculture

Using silvicultural methods to mitigate the effects of weevils essentially involves utilizing shade to mimic the mitigating effects of natural forest processes. Infestations of white pine weevil are known to have occurred after natural disturbance events such as wildfires (Kimoto *et al.* 2000). Silvicultural methods recommend providing overstorey or side shade and using mixtures of tree species. Several researchers (Graham 1918; MacAloney 1930) have observed that conifers growing under deciduous overstorey were subject to lower rates of attack by weevils compared to their counterparts growing in the open. Graham (1926) recommended silvicultural systems that provided shade for young eastern white pines after noting that those growing in the shade, or in high densities, were attacked less by the white pine weevil than trees of the same age growing in full sunlight. MacAloney (1930) concluded that the easiest and most cost-effective way to protect white

pine from the weevil was to grow it in a mixture of tree species that would add value to the final crop. He also noted that successive thinning treatments would be necessary so that pines would not be crowded out (MacAloney 1930). Conversely, Pubanz *et al.* (1999) questioned the use of overstorey for reducing the damaging effects of the weevil. Their study of well-stocked stands on the Menominee Forest in Wisconsin showed that 87.3% of eastern white pines in their samples had an identifiable weevil injury (Pubanz *et al.* 1999). They concluded that volume losses due to attack by weevil have been overestimated. However, Brace (1972) previously estimated of weevil-control could raise the value of white pine by 25%.

Several studies have shown that trees growing in shaded conditions have lower rates of attack by weevils than trees growing in the open (Katovich and Morse 1992; McLean 1994; Taylor and Cozens 1994; Taylor *et al.* 1996). McLean (1989) studied the effects of naturally regenerated red alder, *Alnus rubra* Bong. in 0.14 ha, on growth and attack by weevils on Sitka spruce. Half of the site was cleared of all species and the other half was strip-cleared leaving rows of alder running in a north-south direction. Two stock-types of Sitka spruce were planted in each treatment. The results after eight years showed that one of the stock-types maintained similar height growth in both the open and understory treatment; however, trees growing under red alder had suppressed diameter growth. The trees growing in the open also had more attacks by weevil. McLean (1989) also found that there were higher levels of the dipteran predator *Lonchaea corticis* Taylor in leaders infested with weevils growing in the open compared to those growing in the shade. This was probably due to the fact more food, in the form of weevil larvae, was available to the predators in the open compared to the shade. In a follow up study, McLean (1994) showed rates of attack by weevils to be similar in both understory and open treatments. This was attributed to the clipping of leaders, which reduced the emerging weevil population and to a treatment of sewage sludge, which may have affected their overwintering sites. In a similar study by Taylor and Cozens (1994), side shade from aspen reduced attack by weevils as much as overstorey shade when the strip cuts ran in a east to west direction. Their results indicated that up to 6% reductions in levels of attack by

weevils could be expected five years after the strip cut treatment. Attack levels were 21.3% in the completely brushed area, 14.8% in the side shade treatment and 15.1% in the overstorey shade (Taylor and Cozens 1994).

Researchers have long sought to determine the role of shade and its effects on success of weevils. McMullen (1976) showed that the development of weevils from egg to adult required 785 degree-days above 7.2°C in order for weevils to complete their biological cycle in white spruce leaders under laboratory conditions. The accuracy of this estimate was later tested and confirmed by McIntosh (1997) using internal temperatures of white spruce leaders. Elevation, through its effects on temperature, affects the rate of infestation by weevils (Spittlehouse *et al.* 1994; Taylor 1997). Therefore the presence of overstorey that shades the tree's terminal leader can reduce the degree-days available for brood development.

Sullivan (1961) also showed that reduced temperature under shade resulted in less aggregated feeding on white pine. Alternatively, VanderSar and Borden (1977) showed that weevils have a visual response to Sitka spruce leaders and hypothesized that overstorey trees disturb this silhouette making it difficult for the weevil to locate suitable host-trees. They also demonstrated that weevils have a strong physiological response to light, which makes them climb to the top of leaders after emerging in the spring. VanderSar (1977) also showed that weevils emerging in the spring have a strong phototaxis and negative geotaxis. From his laboratory experiments on excised leaders, he showed that the response to light was the mechanism that primarily governs female oviposition in the spring after overwintering. Shade, created from deciduous overstorey has been shown to reduce overwintering success (Harman and Kulman 1969). Shade may also alter the chemical properties of the leader making them an undesirable host to weevils (Harman and Kulman 1967). Shade also affects the girth of a tree making the diameter of the leader smaller and less likely to be attacked (Sullivan 1961). In addition, shade may delay budburst, causing weevils to seek out trees that are further developed, or which are in synchrony with their spring emergence from overwintering (Hulme 1995, Alfaro *et al.* 2000). A deciduous

canopy also affects the quality of light by disrupting ultraviolet light, which may be an important requirement for weevils when responding to light (Droska *et al.* 1983).

Spacing of trees may also contribute to reduced attack by weevils. Alfaro and Omule (1990) found that increased density, or decreased spacing of young trees, reduced attacks by weevils in Sitka spruce. Their management plan recommended initial spacing of 2.74 m, which should then be thinned at 25 years. Reduced attack by weevils as a result of closer spacing is thought to be due to reductions in temperature, or possibly side shade (Taylor and Cozens 1994). Stiell and Berry (1985) showed that side shade from birch reduced the incidence of attack by weevil on eastern white pine. They found that strip cuts in a white pine plantation permitted between 50-70% of full light, and allowed trees to grow adequately with diminished growth in height, but remained relatively free from weevil damage (Stiell and Berry 1985). Conversely, Hawkins (Pers. Comm. 2000) observed that attacks by weevil increased with the percentage of available stems at narrow spacing in 30-year-old interior spruce plantations growing in the wet cool (wk1) of the Sub Boreal Spruce Biogeoclimatic zone (SBS).

The availability of light potentially can affect 1) the growth and phenology of the tree (Logan 1962, 1969); 2) the insects' ability to perceive the host (VanderSar and Borden 1977); and 3) the temperature required for mating and brood development (McMullen 1976). Light also affects secondary factors, which in turn may impact success of weevils, such as insect predators and parasites that are influenced by temperature. Juvenile spruce are shade tolerant (Logan 1962). Logan (1969) showed that 50% reduction of light did not impede height growth of white spruce by did inhibit diameter growth. VanderSar and Borden (1977) demonstrated that weevils preferred thicker over thinner leaders of Sitka spruce, which may result from growing under reduced light conditions. Messier *et al.* (1999) showed that planting eastern white pine under a hardwood forest reduced competition and protected the trees against damage from weevils. They demonstrated that levels between 10 and 66% full sunlight did not impede growth in the first six years but that total

height and diameter after six years tended to decline sharply when there was 30% or more reduction of full sunlight (Messier *et al.* 1999).

1.5 Economic Significance

Generally, a minimum of two years growth is lost with each successful attack by weevil because the current and previous year's leaders are killed. Cozens (1987) found a 19.5 % re-attack rate on previously attacked trees in interior spruce plantations. Interior spruce is one of the two major commercial species for the central interior, especially in the Prince George Forest District. Since 1984 more than one billion interior spruce seedlings have been planted (Taylor 1997). Most attacks occur in interior spruce stands when they are open grown, between 10-30 years of age and between 2-20 meters tall (Alfaro 1998). However, in high hazard areas, attacks can occur as early as three years at heights of less than 1 m (Hawkins Pers. Comm. 2000). McMullen *et al.* (1987) developed a model to simulate population dynamics of the weevil on Sitka spruce which predicted a 30% reduction in gross volume with severe attack-rates. Alfaro *et al.* (1996b) developed a model to predict volume losses due to attack by weevil called Spruce Attack by weevil (SWAT) which included reductions in net merchantable volume due to defect formation, a factor lacking in the earlier model. The SWAT model works with the TASS, Tree and Stand Simulator, growth and yield model developed by the BC Ministry of Forests to forecast growth. SWAT is used to simulate the damage to trees from attack by weevil (Alfaro *et al.* 1996b). This model has predicted growth losses between 8-65% in the Prince George Forest District, depending on the intensity and duration of attack (Taylor *et al.* 1996).

Large investments have been made in plantations that include planting and vegetation management activities such as brushing or herbicide application. Current legislation in BC restricts the amount of broadleaf species in planted stands to minimum levels. Species such as paper birch, *Betula papyifera* Marsh., are considered weed species and are either treated with herbicide, cut, or girdled to release conifers from competition to meet free-growing requirements

(BC Ministry of Forests 2000). For these investments to be gainfully returned, operational practices for managing attack by weevils need to be incorporated into the free-growing recommendations. Even if spruce trees appear to fully recover from attack, damage incurred at an early age has often already resulted in losses in growth, yield and wood quality. Therefore, the main economic losses incurred from attack by white pine weevil are not realized until time of rotation, due to delay in the harvest.

1.6 Study Objectives

My main objective was to determine if reduced light levels, or shade, created artificially or naturally, lowered success by *P. strobi* on interior spruce trees.

The objective was approached by evaluating the:

1. effects of deciduous overstorey on attack-rate in a young plantation, containing a large endemic population of white pine weevil, and by
2. determining the effects of artificial shade on attack by weevils on planted seedlings.

CHAPTER 2

Impacts of Paper Birch Overstorey on the growth of spruce and attack by the white pine weevil at Sinclair Mills, BC

2.1 Introduction

In central British Columbia, susceptibility of interior spruce stands to infestation by white pine weevil may be increased by current silvicultural practices. These practices are firstly, the planting of a single species in large open clear-cuts, and secondly the management practice of brushing and treating competing vegetation with herbicide to meet Forest Practices Code guidelines (BC Ministry of Forests 2000). Clear-cuts may resemble burned areas which occur in the natural forest (Kimoto *et al.* 2000). Such areas create conditions that allow weevil-populations to flourish because they have easy access to a large number of host terminals, and temperatures are also elevated for brood development to levels which meet the required 785 degree-days above 7.2°C (McMullen 1976). Spittlehouse *et al.* (1994) found that daily average temperatures inside the leader are greater than air temperatures on sunny days and are approximately 1°C on average above air temperatures during the summer months in the interior of British Columbia. Sieben *et al.* (1997) has since revised McMullen's (1976) formula for calculating temperature in the interior of British Columbia by adding 1°C.

It has been hypothesized that removal of broadleaf competitors to enhance growth of conifers may result in increased rates of attack by white pine weevils (Lanier 1983; Alfaro *et al.* 1994; Alfaro 1998). Changes to the BC Forest Act in 1987 promoted the planting of large spruce stands, which must reach a free-growing status 9-15 years after planting (BC Ministry of Forests 2000). Competition from deciduous overstorey, often compromises diameter growth in conifers (Gordon and Larson 1968, page 76), as maximum diameter growth occurs in full sunlight (Lieffers and Stadt, 1994; Wright *et al.* 1998). Therefore, when overtopping brush is removed favourable

habitat is created for the weevil. In addition, ground temperature is increased, allowing for snow to melt earlier and overwintering sites of weevils to be warmed sooner than sites located under deciduous cover.

2.1.1 Objectives

My main objectives of were 1) to compare attack levels of weevil in control and treated stands of interior spruce four years after vegetation removal with glyphosate in the treated stand and 2) to follow weevil-attack rates in both stands over 2 years. In doing so, it would be determined whether removal of mainly paper birch has an impact on rates of attack by weevil and growth variables of interior spruce. Secondary objectives were to quantify differences in light and temperature between open and shaded spruce trees.

2.1.2 Stand History

The study plantation is located approximately 100 km north east of Prince George (Latitude: 54°01' N, Longitude: 121°41' W) at 700 m elevation. It was harvested in the winter of 1987-1988 and broadcast burned in June 1988. The plantation is in the Sub-Boreal spruce very wet and cool (SBSvk 01) subzone (Meidinger and Pojar 1991). The mean annual temperature ranges from 1.3 to 4°C. Annual precipitation ranges from 990 to 1635 mm with only a third falling during the growing season. White pine weevil can have a severe impact on spruce plantations in the SBSvk. In 1989, 77.7 ha of the area was planted with interior spruce (2+1 PBR) seedlot 29164 at 2.5 m spacing, and 14.3 ha was planted with lodgepole pine (1+0 PSB) seedlot 14901 at similar spacing. The plantation was grazed with sheep, for brush control, in the summer of 1992. In July 1996, 24.1 ha of the plantation were treated with the herbicide glyphosate by aerial application to remove competing paper birch, *Betula papyrifera* Marsh. The remaining portion of the block was not treated as competing vegetation was not considered to be a threat to the spruce at that time.

2.2 Methodology

2.2.1 Sampling and Growth

Fifteen, 3.99 m radius plots were systematically selected on 3 transect lines at 25 m intervals in the herbicide treated area of the block (Figure 2.1). Seventeen 5.64 m radius plots were selectively sampled in two regions in control area (Figure 2.1). Larger plots were used in the control area, because the birch was not uniformly dispersed, and therefore larger plots were required to include spruce trees that received different light intensities at the leader within the same area. When the time plots were installed, psuedoreplication was not considered to be an issue as growing environments were similar in both areas (Hawkins and Draper 1991; and Hawkins *et al.* 1996).

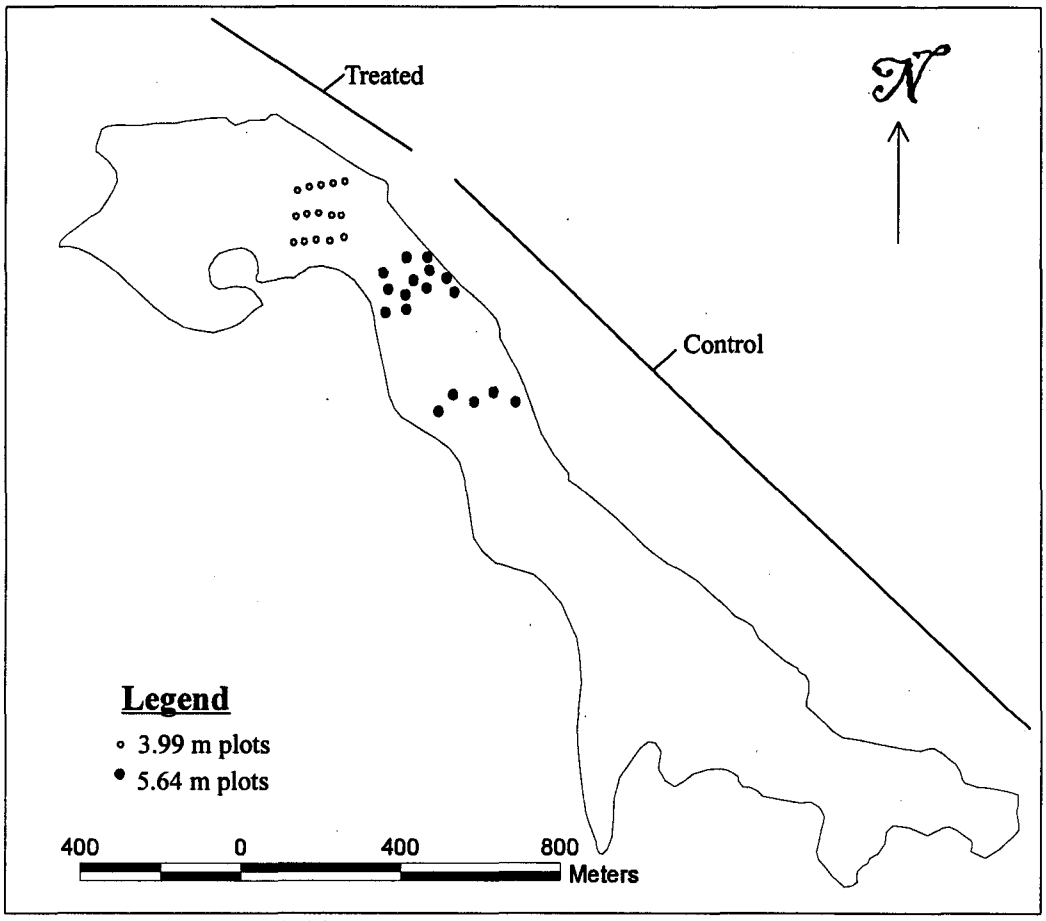


Figure 2.1 Sinclair Mills block layout and sample plot locations.

All naturally regenerated spruce, five in total, and all located in the control area, were removed from the data set. In total there were 193 planted spruce in the control area and 101 in the treated area that were measured for 1) height using a height pole, 2) diameter at breast height (dbh, 1.3m) using a diameter tape, 3) successful attack by weevil (yes or no), defined as leaders killed from attack by weevil in which broods developed (exhibited by shepherds crook or wilted and dying leader), and form. Form was quantified as 0=good, form that would produce a quality butt saw-log; 1=minor defect, such as multiple leaders (but not stag-heads) above the first 2 m of the tree but no visible fork or crook in the stem; or 2=major defect, such as a fork, major crook or stag-head, above 30 cm and below 2 m from the base of the main stem that is seriously impeding growth. Form data were analyzed using Chi-square analysis. All deciduous species in the control plots were measured for height and diameter at breast height. Measurements were repeated in 1999, 2000 and 2001 in the control area and in 2000 and 2001 in the treated area. Data were analysed for differences in height, diameter and diameter increment, between the control and treated areas using Analysis of Variance in GLM, using SYSTAT Version 10 (SPSS, Inc. 2000). In all cases α=0.05

2.2.2 Data Logger

A Campbell (Logan, UT) 21X micrologger was set up in plot 3 of the control stand on May 4, 2001, Julian Day (JD) 124 to monitor 8 temperature sensors. Temperature sensors 1-6 were placed on three separate spruce trees on each tree's terminal leader next to the stem on the north side. Sensors 1 and 2 were placed on the leader of a tree 29736 with shade from surrounding birch trees. Sensor 3 and 4 were placed on a tree 29793 in the open receiving no shade at any time of the day. Sensors 5 and 6 were placed on tree 29738 receiving shade at some parts of the day. Sensor 7 was placed 1.3 m above ground on the north side of the stem of the open tree 29793. Temperature sensor 8 was placed at 1.3 m above ground on the north side of the stem of shaded tree 29736. The data logger was programmed to record temperatures at 1 min intervals and to take the mean temperature for each hour (Appendix I - Data logger programs). It also recorded the maximum and

minimum temperatures during each hour. Three quantum, LI90SB, light sensors (Campbell Scientific, Inc. Edmonton, AB) placed on extension poles in close proximity to the three leaders with temperature sensors, measured continuous light intensity as photosynthetically active radiation (PAR) from which an hourly mean was taken. Quantum sensors were calibrated prior to implementation in the field by Ministry of Forests Research Branch in Victoria (Appendix I). Light readings were taken at the same intervals as temperature readings. The micrologger collected data continuously between May 5-September 10, 2001 (JD 125-253).

Between June 2-7 (JD 153-158) data were lost due to equipment failure. The missing temperature data was interpolated from data on the same days collected with the same model logger at North Willow located approximately 50 km SW of Sinclair Mills, at 650 m elevation. The data for light were estimated based upon data for light collected for each sensor prior to and after the equipment failure. Degree-days were calculated using data collected for temperature between May 5- Sept 10 (JD 125-253): prior to oviposition and up to emergence of adult weevils. The base temperature used was 7.2 C as per the requirements originally described by McMullen (1976). Based on findings from Sieben *et al.* (1997), the formula to calculate degree-days was modified by adding 1°C: $\Sigma(((Tmax+Tmin)/2 + 1)-7.2)/24$. If a value <0 was obtained, it was set to zero before summing each day in the month. Data for light were calculated as a mean for each day.

2.2.3 Leader dissections and parasite identification

In the summer of 2000, 37 attacked leaders, from outside the sample plots in the control area, were clipped below the 1999 terminal and labelled according to whether the leader was from a tree growing in the open, or in full or partial shade. In late August 2000, leaders were placed in individual poly vinyl chloride (PVC) tubes for 1 month. After the adult weevils emerging from each leader were counted, the leaders were dissected and counts were made of un-emerged and

immature adults, as well as larvae of natural enemies, identified as either the predator *L. cortics*, or as unknown hymenoptera parasitoids.

Spruce leaders were also clipped from outside the sample plots in both the treated and control area before emergence of weevils on August 17, 2001. At this time, 20 and 21 successfully attacked leaders, 20 and 21 from the control and treated area respectively and 15 leaders from each area with no visible sign of weevil damage were excised. Adult weevil emergence was quantified by the presence of exit holes, assuming that one exit hole corresponded to one insect. Leaders from both treatment areas were dissected and the number of predators and parasites was counted and identified as above.

Analyses of variance for emergence of adult weevils and number of predators and parasites were made to test for differences between the means for three levels of shade in 2000 and between sites in 2001 using a general linear model (GLM) in SYSTAT Version 10 (SPSS, Inc. 2000). In all cases α=0.05.

2.2.4 Light measurements using Ceptometer

Using 2 AccuPAR (Decagon, Pullman WA) ceptometers, all spruce trees were sampled for light received near the leader-tip of each tree in 2001. Photsynthetically active radiation (PAR) samples were taken, using manual and full-sensor mode to include sensors along the full length of the probe (Anonymous 2001), between 1000 and 1400 on all sampling days. Two samples were collected for each tree, on the south side at approximately mid-length of the terminal leader. Samples were simultaneously taken using a second Ceptometer located in the open. Terminal branches were reached using a 4.8 m orchard ladder. Samples for trees that were above 5.4 m and could not be reached were taken at the maximum height possible. The first samples were taken on 9 and 10 May, 2001 before deciduous bud-break and the second set of samples were taken on 6 and 7 June, 2001 after all surrounding birch had completed bud-flush. The ratio of light received by each tree before and after bud-flush was calculated according to the open light sample taken. Hence

a tree that was in direct light without shade received a ratio of 1, and shaded trees received a value between 0 and 1 (Appendix II).

2.2.5 Light measurements using Plant Canopy analyzer – Leaf Area Index (LAI)

Light transmission was estimated using the plant canopy analyzer 2000 (LI-COR, Inc. Lincoln, NB). Four samples, were taken in a selection of the 5.64 m control plots on June 12 and 13, 2001, and the mean of all samples was taken. Above-canopy readings were made using a 4.8 m orchard ladder. Below-canopy readings were made at 1.3 m. Readings were made in one sensor operating mode, using one above canopy reading and four below canopy readings (Anonymous 1992). Samples were taken from a variety of gaps and levels of shade within each plot. Output is given as a dimensionless figure, ratio m^2 foilage/m^2ground area (Appendix II).

2.2.6 Light measurements using portable spectroradiometer (Li 1800)

Sample measurements under varying canopy conditions were made in plot 2 and in the open on June 4, 2000 using a portable spectroradiometer Li-1800 (LI-COR, Inc. Lincoln, NB) to determine differences in light quality in different parts of the stand. Measurements were made by placing the equipment on a 1 m stand (Appendix II).

2.3 Results

Spruce stocking ranged from 1000 to 1600 sph, with a mean of 1346 sph (± 49.6 SE) in the treated area and from 800 to 1600 sph with a mean of 1135 sph (±56.8 SE) in the control area (Figures 2.2 & 2.3, Table 2.1).

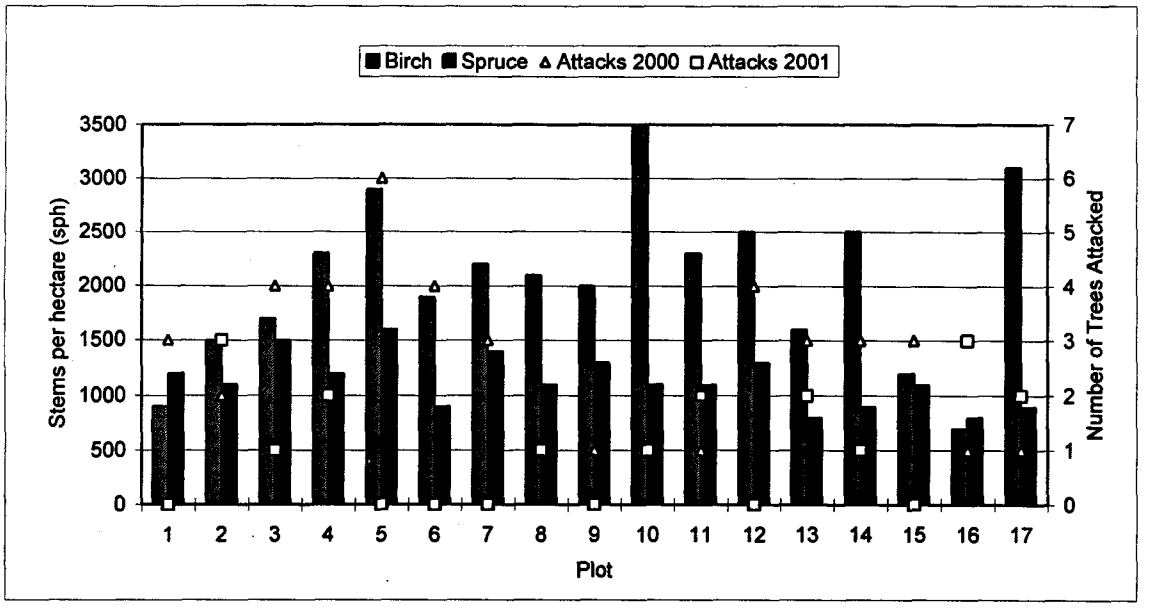


Figure 2.2 Number of spruce and birch stems per ha in control (un-treated) and number of individual attacks by weevils in 2000 and 2001 in sample plots 1-17. Trees attacked by weevils were classified as either successful or unsuccessful.

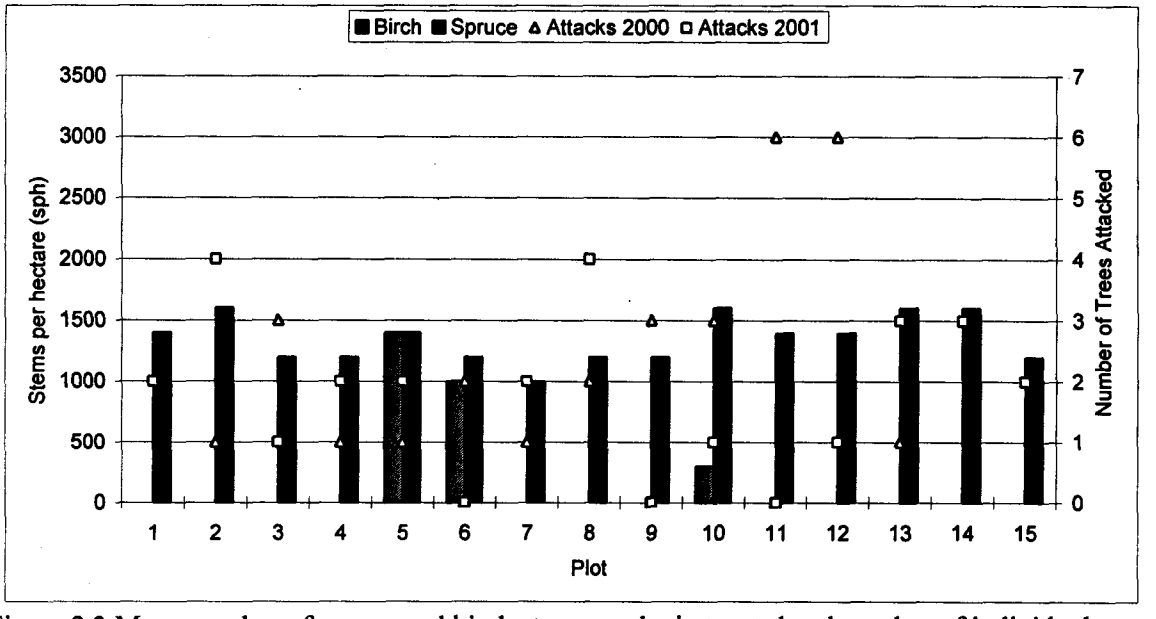


Figure 2.3 Mean number of spruce and birch stems per ha in treated and number of individual attacks by weevils in 2000 and 2001 in sample plots 1-15. Trees attacked by weevils were classified as either successful or unsuccessful.

Table 2.1 Mean (standard error) stems per ha for control and treated areas at Sinclair Mills in May 2001.

	Total	Paper birch	Interior Spruce	Other[2]
Control	3465 (237.8)	2055 (181.9)	1135 (56.8)	276 (77.4)
Treated	1527 (121.3)	180 (1.6)	1346.6 (49.6)	NA

[2]A total of 47 stems, other than paper birch, were found in the control area which included, in descending order of total stems: Willow, *Salix* spp. (19), black cottonwood, *Populus balsamifera spp. trichocarpa* (Torr. & A. Gray) Brayshaw (16), Sitka alder, *Alnus viridis* spp. *sinuata* (Regal) Á. Löve & D. Löve (7), trembling aspen, *Populus tremuloides* Michx., (3) and Douglas maple, *Acer glabrum* Torr. var. *douglasii* (Hook.) Dippel (2).

There were few birch stems in the treated stand, which ranged from 0 to 1400 sph and a mean of 180 (± 1.6 SE) sph in the control area (Figures 2.2 & 2.3, Table 2.1). Spruce diameters increased significantly between years but were not significantly different between treatments (Tables 2.2 & 2.3).

Table 2.2 Mean dbh cm of spruce in control and treated stands in 1999, 2000 and 2001.

	Control			Treated	
	1999	2000	2001	2000	2001
n	193	193	193	101	101
Mean	5.57	6.32	7.36	6.11	6.92
SE	0.15	0.14	0.16	0.22	0.26

Table 2.3 Repeated measures analysis in GLM, results for height, dbh and HDR (height to diameter ratio) in response to fixed effects sources identified in a) between subjects and b) within subjects.

a) Between subjects

Source	df	MS – Height	p-value Height	MS – dbh	p-value dbh	MS - HDR	p-value HDR
Site	1	38.799	0.000	0.785	0.769	5584.367	0.000
Attack 2000	1	29.521	0.000	24.220	0.104	1249.225	0.077
Attack 2001	1	26.610	0.000	0.006	0.980	6261.157	0.000
Site * Attack 2000	1	0.881	0.458	16.355	0.181	559.112	0.236
Site * Attack 2001	1	8.990	0.018	2.770	0.581	1008.801	0.112
Error	282	1.592		9.093		396.834	

b) Within subjects

Source	df	MS (Height)	p-value (Height)	MS (dbh)	p-value (dbh)	MS (HDR)	p-value (HDR)
Time	1	35.794	0.000	60.407	0.000	254.674	0.005
Time * Site	1	0.010	0.748	0.483	0.075	131.018	0.046
Time* Attack 2000	1	.553	0.015	0.274	0.180	192.761	0.015
Time * Attack 2001	1	1.048	0.001	0.038	0.617	105.292	0.073
Time * Site* Attack 2000	1	.027	0.590	0.099	0.419	1.113	0.853
Time * Site* Attack 2001	1	0.202	0.139	0.295	0.164	95.476	0.088
Error	282	.092		0.151		32.486	

Heights were significantly greater in the control than in the treated area, and attacked spruce trees were shorter than un-attacked spruce trees. In terms of the model for height, everything but site by attack in 2000 was significant (Table 2.3a & 2.4).

Table 2.4 Mean height of spruce m in treated and control stands 1999-2001.

	Control			Treated	
	1999	2000	2001	2000	2001
n	193	193	193	101	101
Mean	3.42	3.96	4.57	3.13	3.72
SE	0.06	0.07	0.08	0.07	0.09

There was an interaction between site and attack for the dependent variable (height) in 2001 (Table 2.3a). This occurred because attack rates in 2001 were much lower than in 2000. When time is incorporated into the height model, to examine changes between years, height with time was significant, because trees grew in height between measurement periods, but differences between the control and treated stands were maintained between the years. There also was an interaction between time and attack in 2000 and 2001 (Table 2.3b). This occurred because attack rates differed between the two years at each site and trees that were attacked in 2000 were shorter in 2001.

Diameter, dbh, was not significantly different between sites. The only significant effect occurred when time was incorporated into the model, because the trees grew in diameter between the two years.

Height to diameter ratio (HDR) was significantly different between the control and treated areas. HDR also differed significantly in trees attacked by weevils in 2001, with the control area having a greater HDR than the treated (Table 2.3a). HDR changed with time and there were interactions between time and site, and time and attack in 2000 (Table 2.3b). These interactions appeared because the mean diameter was larger in the control than in the treated area. There was little difference in diameter and height increments between treatments (Table 2.5).

Table 2.5 Mean diameter and height increment of spruce in 2001 for treated and control stands.

	Diameter Increment (cm)		Height Increment (m)	
	Treated	Control	Treated	Control
n	101	193	101	193
Mean	0.93	1.02	0.63	0.60
SE	0.07	0.03	0.04	0.03

Birch (Table 2.6) were about 1.4 m taller and 2.5 cm smaller in diameter than spruce (Tables 2.2, 2.4) in the control area. Other species did not contribute significantly to vertical structure of the stand and were not included.

Table 2.6 Mean, minimum and maximum height and dbh of birch in 1999, 2000 and 2001.

	Height (m)			dbh (cm)		
	1999	2000	2001	1999	2000	2001
n	340	349	349	340	349	349
Min	1.50	2.00	2.80	1.00	1.20	1.50
Max	8.00	8.50	8.90	7.80	10.30	11.80
Mean	4.48	4.95	6.09	3.94	4.35	4.92
SE	0.05	0.05	0.05	0.07	0.07	0.08

Attack rates varied by treatment (Table 2.7) but did not vary by plot with each treatment over the two-year study period (Figures 2.2 and 2.3).

Table 2.7. Mean yearly rates of attack by weevil on spruce (percent of total sample trees attacked by weevils, resulting in death of leader) in control and treated plots.

	Control			Treated	
	1999	2000	2001	2000	2001
Percent Attack	16%	23%	9%	36%	27%
SE	0.27%	0.36%	0.26%	0.42%	0.34%

Over the 2-year study period levels of attack were a mean 16.1% in the control and 31.1% in the treated plots (Table 2.7). Rates of attack for 1999 are only given for the control area as these plots were measured early in the spring of 2000, before attack, or tree-growth had occurred while plots in the treated area were not measured until later in the season.

Based upon Chi-square analysis percentage of trees with poor and good form classes varied significantly (Table 2.8) between each treatment area.

Table 2.8 Trees in control and treated area with good, moderate and poor form and significant difference between each area by form class based on Chi-square analysis.

Form Classes	% Trees Treated	% Trees Control	Chi-square	df	p-value
Good (0)	25	55	16.6	1	0.0002
Moderate (1)	35	35	0.24	1	0.9900
Poor (2)	40	10	17.52	1	0.0002

Percentage of major defects was greater in the treated area compared to the control. Major defects accounted for 10% of trees sampled in the control *versus* 41% of trees in the treated area. Trees with good form made up 55% of trees sampled in the control area *versus* 25% of trees in the treated area. Moderate defects, damage caused by weevils on spruce above 2 m in height, were not different between the two sites, with approximately 35% moderate defects for trees sampled in each area.

From measurements taken using the ceptometer, there was a mean 23% reduction in light intensity for the control stand after bud-break (Table 2.9).

Table 2.9 Mean light ratio (tree/open) received at leader level, before[1] and after deciduous leaf-out in control plots.

	May 2001	June 2001
Mean of 193 samples	0.94[1]	0.71
SE	0.01	0.02

[1] Mean light ratio was less than 1 before deciduous leaf-out because stems and branches caused shade

Mean leaf area index (LAI) for the control plots was 2.19, indicating a medium amount of foliage coverage overall. The variation in measurements ranged from 0.8, little or no cover to 4.75, indicating high levels of deciduous cover at the location where the reading was taken (Figure 2.4).

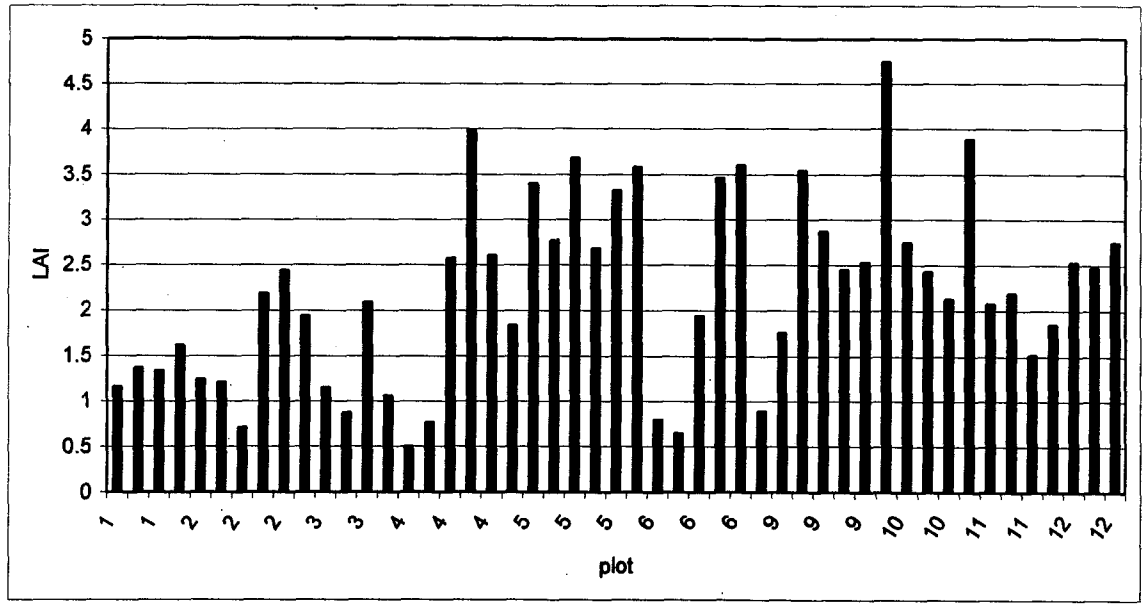


Figure 2.4 Leaf area index (LAI) for control plots 1-6 and 9-12 taken on June 12 and 13, 2001.

In the open there were 697.6 degrees of temperature accumulated, above the threshold 7.2°C during the sampling period. There were 657.9 and 654.0 degree-days accumulated above 7.2°C between May 5-September 20 (JD 125-263), on leaders of the partially shaded and mostly shaded trees respectively. Mean intensity of light at the leader decreased from the open-tree to the mostly shaded tree and there was a greater difference between partial and mostly shaded trees in contrast to degree-days. (Figure 2.5)

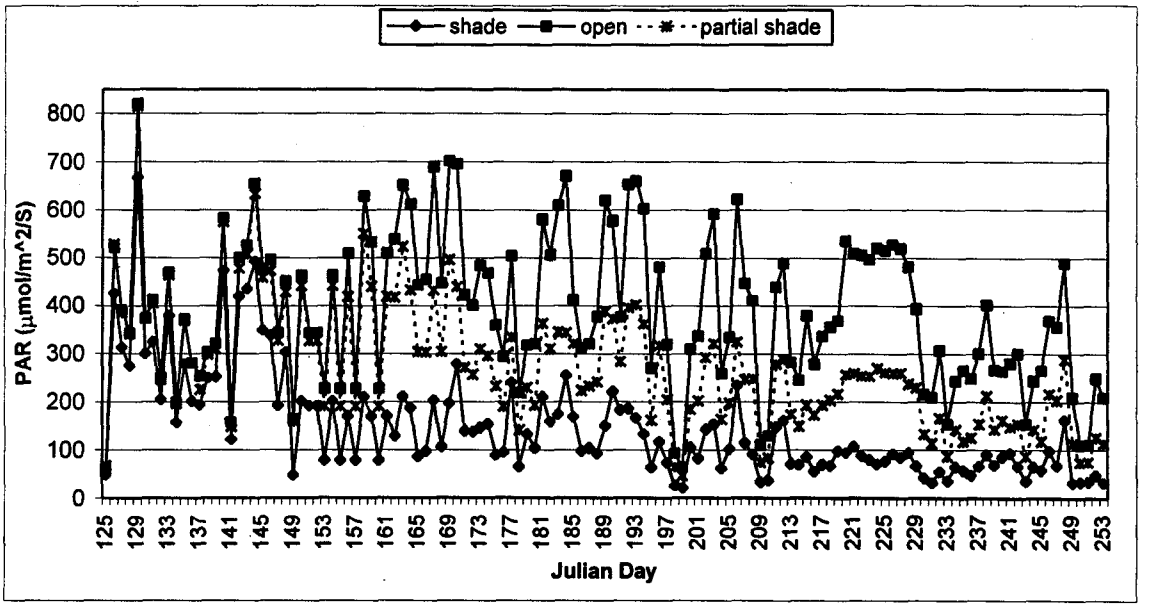


Figure 2.5 Photosynthetically active radiation (PAR) received in 2001 from May 10-Septermber 10 (JD 125- 253).

From the 41 successfully attacked leaders dissected in 2001, there was no significant difference between sites for the number of dipteran (predator) larvae or parasite larvae (Table 2.10).

Table 2.10 Comparison of mean number of diptera (predators) and parasites dissected from leaders in control and treated areas in 2001.

	Control		Treated	
	Diptera	Other	Diptera	Other
n	20	20	21	21
Mean	23.7	2.7	21.8	0.3
SE	6.7	0.7	5.4	0.1

Mean number of adult weevils emerging from the leader was greater in control compared to the treated areas in 2001 (Table 2.11). There was no significant difference among the open, partially shaded and fully shaded trees for weevil emergence or parasite number in 2000 (Table 2.12).

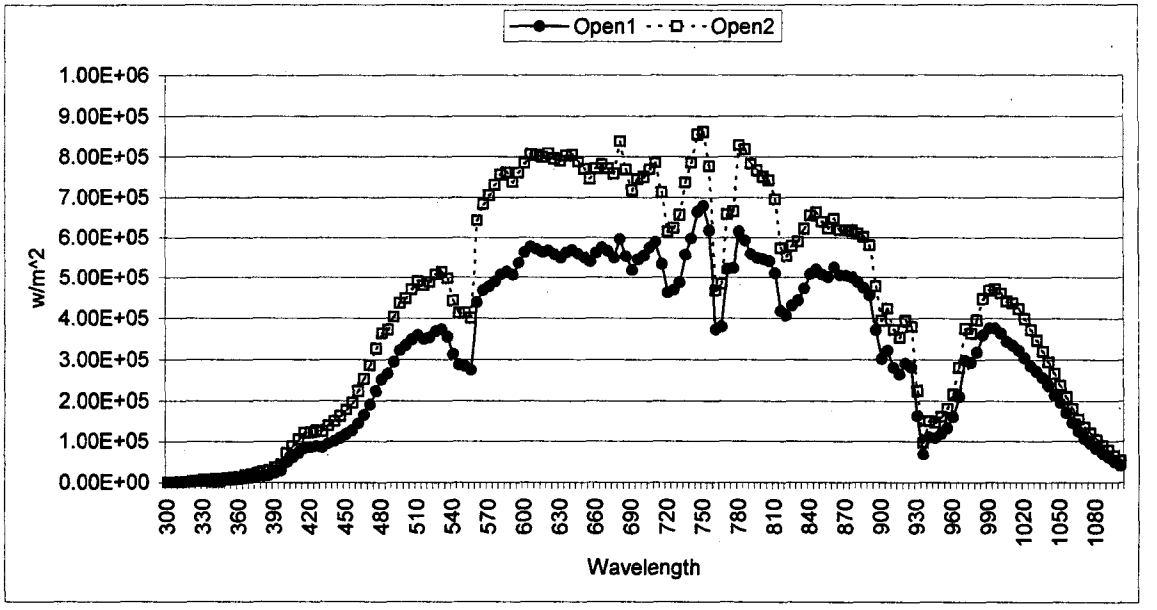
Table 2.11 Number of adult weevils emerging from leaders clipped in control and treated areas during 2001.

	Control	Treated
n	20	21
Min	0.0	0.0
Max	8.0	9.0
Mean	2.1	0.9
SE	0.6	0.5

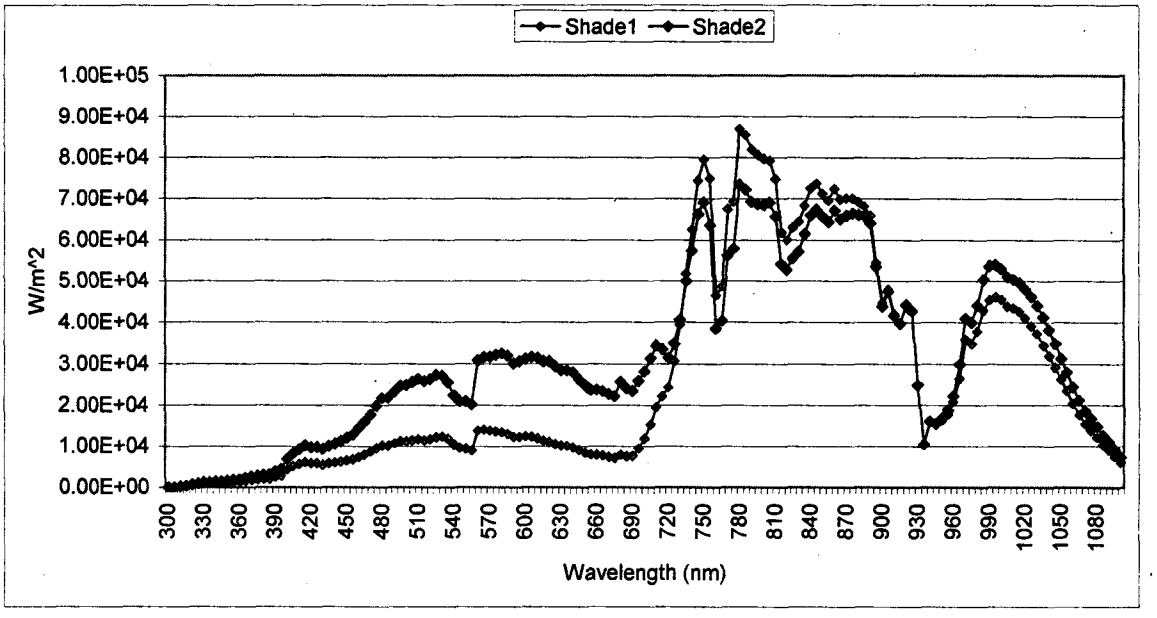
Table 2.12 Mean number of live weevils, predators and parasites dissected from leaders clipped in control plots in 2000; shade, partial shade and open in 2000.

	Shade		Partial Shade		Open (no shade)	
	Adult Weevils	Parasites & Predators	Adult Weevils	Parasites & Predators	Adult Weevils	Parasites & Predators
n	12	12	12	12	13	13
Mean	4.4	11.9	5.47	9.5	7.2	12.1
SE	1.5	3.9	1.4	3.3	1.5	3.1

Spectral light quality changed under the canopy in comparison to the open, particularly in the far-red and blue region (Figure 2.6).



a) Open



(b) Shade

Figure 2.6 Light transmission in W/m^2, by wavelength in plot 4, for trees in the open (a) and in shade (b) on June 1, 2000; between 0956-1030.

2.4 Discussion

2.4.1 Growth of Spruce

In contrast to the contention that an overstorey of angiosperm trees reduces growth in both height and diameter of conifers (Logan, 1969; Stewart *et al.* 1984; Leiffers and Stadt 1994; Oliver and Larson 1996 page 75; Wright *et al.* 1998), the presence of an average 2055 sph of birch, up to a maximum 3500 sph, in the control area at Sinclair Mills did not appear to reduce growth of spruce in either height or diameter. Taylor *et al.* (1996) noted a trade off between overstorey shade in a primarily aspen, *Populus tremuloides* Michx., canopy and height growth of interior spruce. The mean diameter increment of the spruce was not different between the control and herbicide-treated stands (Table 2.2), and the lower height of spruce in the treated areas (Table 2.4) was likely due to attacks by weevils, because height increment did not vary between areas.

Shade generally causes an etiolated effect in trees (Logan 1969). They grow taller with a decreased diameter because carbon is first allocated to height growth and then to diameter growth in limiting situations (Gordon and Larson 1968; Rangnekar and Forward 1973). In my study, the 23% lower light level in the control than in the treated area, may not be enough to etiolate 10-12 year-old interior spruces. Logan (1969), Leiffers and Stadt (1994) and Wright *et al.* (1998), found that white spruce seedlings growing under 50% and full sunlight achieved similar height growth. It is generally accepted that the best diameter growth in spruce occurs in full sunlight (Leiffers and Stadt 1994; Wright *et al.* 1998). However, Eis (1967) suggests a diameter growth threshold of 60% full sunlight for white spruce. The hypotheses that growth of white spruce >10 years old is optimal under full sunlight (Logan 1969; Eis 1970) is supported by smaller height and diameter of white spruce growing under a trembling aspen canopy than in the open (Johnson 1986; Yang 1989).

My results suggest that the growth of interior spruce under a paper birch canopy is very different from that under a trembling aspen canopy. This difference may be due to a variety of factors. Silhouettes of aspen and birch are different, with aspen having a greater crown area than birch (Farrar 1995). The estimated site index, SI_{50} 28m (estimated height of trees, 28 m at 50

years), using the spruce site index equation (Nigh and Löve 2000) is high compared to a lower site indices in found in studies with an aspen canopy (Taylor and Cozens 1994). Benefits from the presence of birch may also be derived from ectomycorrhizal fungi that serve as a nutrient gathering interface in the soil (Smith and Read 1997). Comeau (1996) reported increases in yield of mixed stands with a birch component compared to yields in pure conifer stands. Simard *et al.* (1997) showed a mutualistic association with mycorrhizae, between paper birch and Douglas-fir. Simard and Hannam (2000) reported that growth of 8-year-old interior spruce in the Interior Cedar Hemlock (ICH) subzone, was not constrained by competition with paper birch <4000 sph. Because paper birch, at its present density on the Sinclair Mills site, appears to significantly aid spruce growth and development and increase total site yields, treatment with herbicide for conifer-release at this site does not appear to be justified.

2.4.2 Attack on Spruce by Weevils

The most reasonable explanation for lower attack by weevils in the treated than the control area (Table 2.7) is that population of weevils in the control area is lower in comparison to the treated area. Although no difference was found in adult insects emerging from individual leaders, there were many more spruce trees attacked by weevils in both 2000 and 2001 in the treated site than in the control. However, taking into account 1135 sph at 16.1% attack rate per year and 2.1 weevils emerged per leader in the control area, and 1346 sph, at 31.1% attack rate and 0.91 emergent weevils per leader in the treated area (Table 2.1, 2.7, 2.11), there would be 384 and 380 emergent weevils/ha/yr in control and treated areas respectively. The question that must therefore be asked is what determines the difference in attack success between the two areas?

The sample tree that was directly in the open received 697.6 degree-days above 7.2°C, or 89% of the required 785 degree-days (McMullen 1976; McIntosh 1997) between May 5-Septermber 10 (JD 125-253). The shaded trees received approximately 41 degree-days less than the open tree, or about 83% of the degree-day threshold for life cycle completion, than the open tree.

The temperature requirements were not met at Sinclair Mills, even though the revised formula by Sieben *et al.* (1997) was used. Insect emergence was still observed in both the control and the treated areas, but may have been higher if degree-day temperatures were greater. Error in field equipment and sensor-placement would have factored into the final heat-sums. Elements such as wind velocity and humidity, which were not measured, may have also affected the readings of the temperature sensors. However, temperature, may have played a part in reducing brood development in 2001 as the rates of attack were significantly lower in the control (9%), compared to the treated area (27%). Rates of attack in the treated area were very high which leads to speculation that physical factors, other than temperature, need to be considered in the role of weevils attacking spruce.

It was observed that weevils continued to feed, mate and oviposit well after deciduous leaf development had occurred in the control area. It was also observed, in both years, that weevils emerged and started feeding and mating sooner in the treated than in the control area. These differences may have more to do with the soil temperature than a direct result of differences in light because exposed soil tends to warm sooner than shaded soil (Stathers and Spittlehouse 1990). Sites where weevils overwinter would therefore warm earlier in open compared to sites located in the shaded stands. The exposure to the open areas also allows for earlier snow melt, thus making water available to the trees sooner, thereby allowing for earlier development. In this study, spruce trees in the treated area started bud-break one to two weeks before those in the control area. According to Hulme (1995) spruce that flush later are more susceptible to attacks by weevil than those that flush earlier, which may explain the greater emergence of weevils from attacks that did occur in the control area.

The quality of light was different when weevils were still feeding and laying eggs (Figure 2.6). Portions of the spectrum diminished under shade of the birch, may affect the ability of weevils see the terminal, particularly because the near infrared spectrum became one of the more prominent wavelengths under the birch canopy.

The lack of any difference in number of parasites and predators dissected from the clipped leaders between the shaded and open leaders was unexpected. McLean (1989) found more parasites in the open than on Sitka spruce growing under red alder. Previous studies (Stevenson 1967; Nealis 1998) have speculated that predators and parasites may be a significant factor in controlling weevil populations. My results support this hypothesis in part because numbers of emerged weevils were lower (Table 2.11). The greater number of parasites and predators in the 2000 leaders than in the 2001 leaders may be due to temperature variation between 2000 and 2001.

The greater percentage of trees with very poor form in the treated than control stands can be attributed to the many years of successive attack by weevils. Although the estimates of historical attack, 75% and 80% for control and treated stands respectively, do not vary greatly between sites the exact number of times a tree has been attacked cannot be assessed without destructive sampling. Trees with minor damage did not vary significantly between stands. Because both the control and treated areas were relatively similar before the 1996 treatment with herbicide, apparently it took only 4-5 years for impact levels of attack in the treated and control areas to diverge.

Tree vigour, or growth appeared to have an impact on levels of attack only in 2001 (Table 2.3) as HDR did not significantly affect levels of attack in 2000. Diameter increment was not significantly different between the control and treated areas. Therefore, the effects of growth rate on attack, are only speculative. King *et al.* (1997) noted that the fastest growing trees of interior spruce were attacked more frequently than slow growing trees. However, faster growth has also been linked with greater resistance to attack by white pine weevil (Kiss and Yanchuck 1991). At Sinclair Mills, attack may be affected by rate of spruce-growth. The reason that HDR was only significantly related to attack in 2001 is unknown. Timing of spruce bud-break, or some other factor, may also be key in determining whether weevils successfully attack the spruce. Because the spruce trees appear to break bud later in the control than in the treated area, yet manage to have an equal growth increment, may mean that the spruce in the control are growing at a faster rate

through the season. The less likely alternative is that spruce in the control plots maintain their growth later into the season than the spruce in the treated area. This latter explanation is unlikely as conifers are cued by photoperiod to complete growth (Dormling 1989) and the spruce seed source was the same for both the control and treated areas. The former explanation could only hold if the growth environments were significantly different, which they were with respect to light and temperature.

2.5 Conclusions

Interior spruce tree form and mean tree height were significantly better and rates of attack by weevils were significantly less in the control area. Birch densities in the control ranged from 700 to 3500 sph and mean total densities of spruce and birch were 3465 sph. These findings have important ramifications for forest policy in British Columbia. The control area does not meet free-growing criteria for competition of deciduous species and the treated area was not free-growing due to levels of attack by weevil. Interspecific competition at the observed densities did not reduce crop tree growth at 13 years, but appears to have a negative impact on attack by white pine weevil. Further studies are necessary to determine the specific mechanisms which result in reduced attack by weevil under paper birch or other species that form deciduous canopies. Studies like this will need to be followed in the long-term to determine the if there will be an impact on volume of spruce at the time of harvest. More importantly, replicated experiments need to be installed, or replicates already established need to be measured.

CHAPTER 3

Open pollinated interior spruce families and resistance to white pine weevil under varying degrees of shade

3.1 Introduction

The Prince George Forest Region has approximately 300,000 hectares of interior spruce, plantations, >34,000 ha of which are at risk to attack by the white pine weevil (Taylor *et al.* 1996). Employing a combination of silvicultural tactics, which include the planting of spruce stock with known resistance traits, should mitigate damage caused by the weevil (Alfaro *et al.* 1995).

The objectives of this investigation were to determine 1) if resistance to white pine weevil could be shown at a young age in progeny trees in families with known weevil resistance, 2) if varying light levels affected feeding and oviposition behaviour of white pine weevils and if light levels affected growth of spruce, and 3) if there were interactions among spruce family, light level, and attack by weevil. I hypothesized that trees subjected to artificial shade would be attacked less than open-grown trees, and eggs would be deposited in a more dispersed manner along the terminal. It was also believed that trees from families with a high resistance-ranking would be attacked less by weevils, regardless of shade or light treatment.

3.2 Methodology

Seeds from trees of 40 open pollinated families of interior spruce, Vernon Seed Orchard #214, were collected by family in 1996. All of the families were ranked according to growth and resistance to *P. strobi*. Seeds were sown and grown in 1997 at the JD Little Forestry Centre, near Prince George. Seedlings were spring planted, from 415B 1+0 stock, in two trials near Prince George in 1998. At Pass Lake, 90 Km northeast of Prince George (Latitude: 54°15' N, Longitude: 121°42' W ~1000 m in elevation) in the SBSvk 01, the layout included 160 squares with 25

seedlings each planted 2.5m apart. Each family was replicated four times. Five of the 40 families planted at this location were selected for testing in 1998, based upon their ranking for weevil resistance by the Ministry of Forests (Table 3.1).

Table 3.1 Selected families showing original white pine weevil resistance ranking, breeding value, and location of original plus-trees and successful attack by weevil in 2000.

Family	Weevil Resistance Ranking[1]	Breeding Value[2]	Elevation (m)	Latitude	Longitude	No. trees successfully Attacked in 2000
16	4 (high)	18.7	685	53° 56'	122° 06'	5
21	6 (high)	19.8	732	53° 54'	122° 02'	3
27	38 (low)	16.1	763	53° 53'	122° 18'	5
139	2 (high)	25.4	899	53° 47'	122° 25'	6
140	31 (low)	23.9	777	52° 47'	122° 01'	4

[1] Relative ranking of 173 families
[2] Expected percentage increase in volume at rotation

Two shade treatment levels (65 and 28% full light, 1 and 2 layers of shade cloth, corresponding to light and heavy shade respectively) were set up over the 20 randomly selected seedlings (10 per treatment) in each family and another 10 seedlings per family were randomly selected as open-grown controls exposed to full light. Light and heavy shade treatments were set up using neutral density greenhouse shade cloth, set at 45° to the south, over posts set to the east and west of each tree. East and west aspects were also appropriately shaded. Heights and leader diameters of all seedlings were taken for 1999 growth on May 12, 2000. Trees were again measured for height and diameter at the end of August 2000, and only for height in August 2001.

Five weevils collected from a nearby naturally infested stand were placed on 15 (5 per light treatment) of the 30 randomly selected spruce-seedlings in each family, on May 17, 2000, before they broke bud. Oviposition punctures, determined by the black fecal plugs, was categorized as; absent, dispersed along the stem of last year's terminal growth or aggregated within 3 cm of the

terminal bud of the 1999 leader. Punctures were counted weekly for four weeks and final categories were assigned on June 19, 2000.

Temperature was averaged hourly using a Campbell (Logan, UT) 21X micrologger, and the daily treatment mean temperature above 7.2°C was determined from May 15-September 5 (JD 135-248) using the formula: $\Sigma(((Tmax+Tmin)/2 + 1)-7.2)/24$. Light quality was sampled under each light regime on June 4, 2000 using a portable spectroradiometer Li-1800 (LI-COR, Inc. Lincoln, NB). Successful attack, denoted when a tree's terminal leader was girdled and dead or dying from attack by weevil, was determined in late August 2000.

3.2.1 Analyses

Factorial repeated measures ANOVAs using SYSTAT Version 10 (SPSS, Inc. 2000) were done on leader growth and diameter. The independent variables were family, shade treatment, weevil seeding and their interactions. Kruskal-Wallis analyses were also done for attack success and oviposition density, on trees that had been seeded with weevils. Chi-square analyses were used to determine difference in dispersal of oviposition punctures for each level of shade. In all cases $\alpha=0.05$.

3.3 Results

There was no significant difference in height or height growth among the five families (Tables 3.2, 3.3a).

Table 3.2 Mean height (cm ±SE) of 30 spruce trees from each of five families at Pass Lake in 1999, 2000 and 2001.

Family and Resistance Level		Mean Height (cm ±SE) by year		
	Treatment	1999	2000	2001
16 (high)	Control	45.5 (1.5)	57.9 (2.3)	70.1 (3.4)
	Weevil[1]	45.3 (1.9)	56.7 (3.4)	64.9 (5.6)
21 (high)	Control	44.1 (0.9)	58.7 (1.0)	70.1 (2.1)
	Weevil[1]	45.4 (1.6)	59.5 (1.6)	68.0 (3.4)
27 (low)	Control	44.2 (1.0)	56.3 (1.6)	68.1 (2.8)
	Weevil[1]	45.0 (1.5)	52.8 (2.3)	58.0 (2.8)
139 (high)	Control	43.1 (1.2)	56.6 (1.7)	66.6 (3.2)
	Weevil[1]	43.2 (1.6)	55.4 (2.7)	59.6 (5.6)
140 (low)	Control	43.9 (1.2)	55.9 (1.8)	68.5 (2.9)
	Weevil[1]	42.6 (2.0)	54.3 (2.4)	61.8 (3.1)

[1] Trees in weevil treatment seeded with weevils before bud-flush in 2000.

Table 3.3. Repeated measures analysis of variance results for height in 1999, 2000 and 2001, in response to resistance, shade treatment and weevil seeded trees (fixed effects) sources identified in a) between subjects and b) within subjects.

a) Between Subjects

Source	SS	df	MS	F	p-value
Resistance	260.88	4	65.22	0.335	0.854
Shade	87.90	2	43.95	0.226	0.798
Weevil	1885.88	1	1885.88	9.697	0.002
Resistance*Shade	2349.79	8	293.72	1.510	0.162
Resistance*Weevil	662.75	4	165.69	0.852	0.495
Shade*Weevil	158.88	2	79.44	0.408	0.666
Resistance*Shade*Weevil	2646.74	8	330.84	1.701	0.106
Error	21199.29	109	194.49		

b) Within Subjects

Source	SS	df	MS	F	p-value
Time	40700.56	2	20350.28	332.196	0.000
Time*Resistance	194.61	8	24.336	0.397	0.921
Time*Shade	154.41	4	38.60	0.630	0.641
Time*Weevil	2252.29	2	1126.15	18.383	0.000
Time*Resistance*Shade	1644.38	16	102.77	1.678	0.052
Time*Resistance*Weevil	635.71	8	79.46	1.297	0.246
Time*Shade*Weevil	46.09	4	11.52	0.188	0.944
Time*Resistance*Shade*Weevil	1175.51	16	73.47	1.199	0.270
Error	13354.66	218	61.26		

Weevil-seeded trees were significantly shorter than control trees (Table 3.3a). Within-subject tests for height, using repeated measurements in ANOVA, show a significant difference with time, because trees grew between measurement periods (Table 3.3b). Repeated measurements also revealed that there was an interaction between time and trees that had been weevil-seeded in between subject tests (Table 3.3b). This occurred because the trees that were attacked in 2000 were shorter, resulting in the interaction between time and seeding with weevils.

There was a significant difference in leader basal diameter among families, in both 1999 and 2000 (Table 3.4 and 3.5).

Table 3.4 Analysis of variance for girth (leader basal diameter) in 1999 between Resistance (family), shade treatment and weevil seeded trees and their interactions.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	p-value
Resistance	9.387	4	2.347	3.047	0.020
Shade	1.002	2	0.501	0.651	0.523
Weevil	0.068	1	0.068	0.088	0.767
Resistance*Shade	3.217	8	0.402	0.522	0.838
Resistance*Weevil	1.728	4	0.432	0.561	0.691
Shade*Weevil	0.677	2	0.338	0.439	0.645
Resistance *Shade*Weevil	1.687	8	0.211	0.274	0.973
Error	92.419	120	0.770		

3.5 Analysis of variance for leader basal diameter in 2000 between Resistance, shade treatment and weevil seeded trees and their interactions.

	Sum-of-Squares	df	Mean-Square	F-ratio	p-value
Resistance	10.492	4	2.623	3.637	0.008
Shade	1.837	2	0.918	1.274	0.284
Weevil	2.481	1	2.481	3.440	0.066
Resistance *Shade	5.703	8	0.713	0.988	0.449
Resistance *Weevil	4.879	4	1.220	1.691	0.157
Shade*Weevil	0.729	2	0.365	0.506	0.605
Resistance *Shade*Weevil	2.503	8	0.313	0.434	0.898
Error	75.718	105	0.721		

All other variables were not significant and there were no interactions between them. Repeated measures were not used for girth as measurements were taken at different points of the leader in each year. Family 139 had the greatest leader diameter in 1999 and 2000 (Table 3.6).

Table 3.6 Mean leader diameter (mm ±SE) in 1999 and 2000 for 30 spruce trees from each of the five families sampled at Pass Lake.

Family and Resistance	Mean Leader Basal diameter (mm ±SE)	
	1999	2000
16 (high)	4.0 (0.1)	3.0 (0.1)
21 (high)	4.3 (0.1)	2.6 (0.1)
27 (low)	4.5 (0.2)	3.0 (0.2)
139 (high)	4.7 (0.2)	3.3 (0.2)
140 (low)	4.6 (0.2)	3.2 (0.2)

There were 832.0, degree-days above 7.2°C for the open grown trees, and 789.1 and 707.0 degree-days under light and heavy shade respectively, approximately 94.8% and 84.9% of the heat received in the open. Differences in light intensity under each treatment, throughout the season are seen in Figure 3.1.

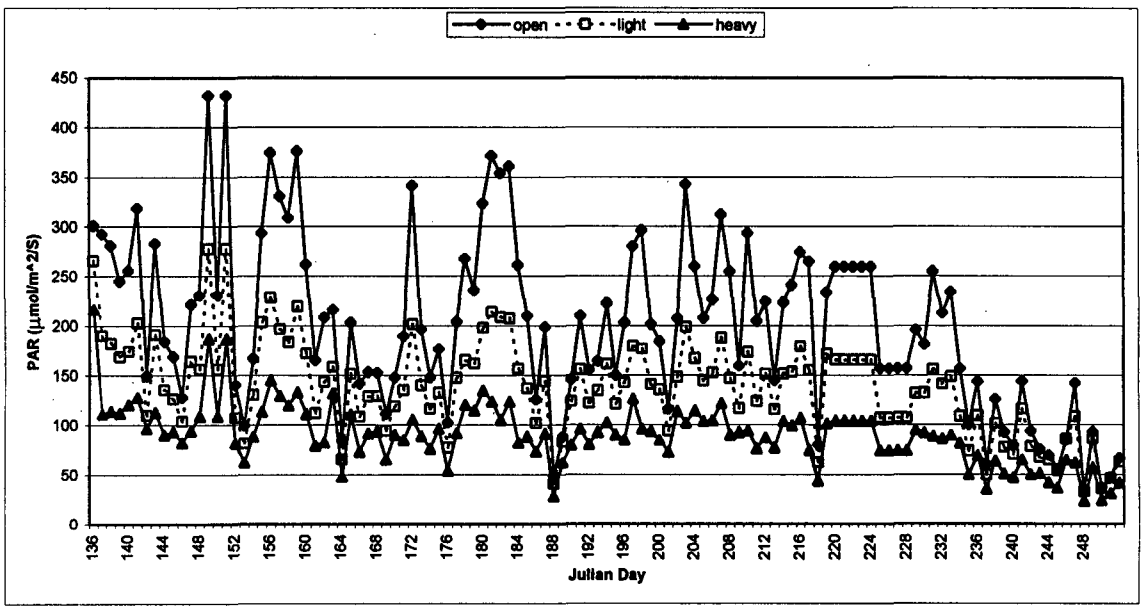


Figure 3.1 Mean light intensity (PAR) for each shade treatment (light and heavy) and in the open at Pass Lake for the May-July 2000 period.

Light quality was not changed under each shade treatment indicating that the shade cloth was neutral density (Figure 3.2).

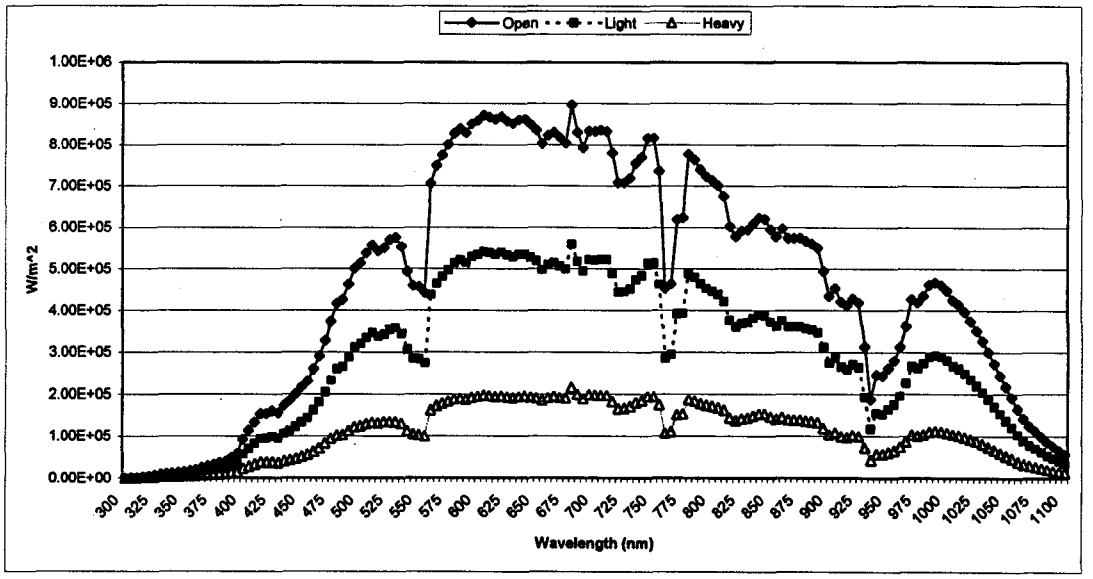


Figure 3.2 Energy of light by wavelength in the open and under light and heavy shad, June 1, 2000, 11:00 at Pass Lake.

In 2000, 23 successful attacks were distributed almost uniformly among the five families (Table 3.1). There were no differences in the number of successful attacks in the heavy shade compared to the light shade or open treatments: 6 *versus* 9 and 8 attacks respectively. There was a significant difference among the three light treatments for oviposition category (Table 3.7).

Table 3.7 Kruskal-Wallis test statistic and significance for non-parametric tests between number of successful attacks and resistance, shade and oviposition pattern (category) and resistance and shade treatment.

Dependent Variable	Grouping Variable	Kruskal-Wallis Test statistic χ^2	p-value
Attack Success	Resistance	1.103	0.894
Attack Success	Shade	0.865	0.649
Oviposition category	Resistance	3.482	0.481
Oviposition category	Shade	6.173	0.046

Trees under heavy shade had the largest number of trees with no oviposition and the lowest level of aggregated oviposition punctures. In contrast, the greatest number of trees with aggregated oviposition punctures were growing in the open (Table 3.8).

Table 3.8 Number of trees in each shade level per oviposition category, showing significant effects of shade on oviposition.

Oviposition Category	Number of trees per Shade Level			Chi-Square	df	p-value
	Open	Light	Heavy			
Absent	12	9	18	12.880	2	0.002
Dispersed	4	12	5	5.199	2	0.055
Aggregated	9	4	2	7.119	2	0.037

3.4 Discussion

Early performance results from this trial were not consistent with the original breeding value and weevil rankings. Family 27, which had the lowest resistance-ranking and breeding value, had relatively large diameter-growth. Family 16, which was ranked high ranking for resistance to weevils had the lowest overall leader-growth. These findings may be due to several factors. All families were originally tested under well-maintained research conditions unlike the operational conditions at Pass Lake. All families except 139 were from low and mid elevation sites and movement to an elevation of 1000m at Pass Lake exceeded the 200 m maximum change recommended for interior spruce (Anonymous 1995). A nursery-effect, influencing the health and vigour of the seedlings after leaving the nursery, may have been present in the field, three years after planting, resulting in trees in families with low breeding values to perform better than expected.

Resistance by plants to insect attack can result from a combination of many traits. Some of the factors that influence these traits are related to growth rate (Kiss *et al.* 1994; King *et al.* 1997). The trees in this study may not be old, or large, enough to yet exhibit some of these resistance traits. Previous rankings for resistance were based on older trees performing well in areas where attack by weevils occurred endemically. Presence of white pine weevils reduced leader basal diameter and leader growth in some families even though the insect did not cause visible damage (Table 3.4 & 3.5). However, this effect was not significant in all families. Reduction in girth may be due to adult insects feeding on the stem or by larvae, having fed inside the stem but not developing fully after oviposition. Predators such wasps and flies, are known to kill weevil-larvae (Hulme and Harris, 1988) and may have contributed to the lack of successful attack by weevils.

Past studies have shown that shade reduces the diameter growth of the leader making it an unfavourable host for the weevil (Sullivan 1961). Diameter growth in this study was not significantly affected by light level but instead by family. The trees from this study may have been too small to have an effect on whether or not weevils choose them as hosts. However, in a study by

Kiss *et al.* (1994), it was shown that weevils attacked interior spruce regardless of leader length or diameter, and genetic resistance was the greatest determinant of attacked seedlings. In my study, weevil feeding was observed on most of the weevil-seeded trees even when no oviposition punctures were observed.

Density of oviposition punctures differed significantly by light treatment levels, although attack success did not. Successful attack is ultimately the most important criterion in determining the effectiveness of shade as a control measure. However, this still may have implications for planting spruce under deciduous cover, if future studies show that natural shade reduces success of attack and growth of spruce is not reduced.

The level of shade did not affect the growth of spruce. This is not surprising as previous results (Logan 1969) have shown that white spruce planted under 50% light intensity can reach optimal height-growth. The trees growing in the open, or full light condition, had the largest number of trees with aggregated oviposition. This is significant because the insect must lay eggs that are dense enough for hatching larvae to find one another to form a communal feeding ring (Silver 1968). If eggs are laid dispersed along the stem, the larvae become drowned in the trees' resin and the leader continues to grow (Silver 1968). Therefore, the light shade treatment (65% full light) should not reduce spruce height growth but significantly reduce aggregated weevil oviposition, while the heavy shade treatment (28% full light) will meet reduced attack by weevil objectives but reduce spruce growth based upon Logan's (1969) observations.

McMullen (1976) found that 785 growing degree-days above 7.2°C were needed in order for weevils to develop in the leaders of white spruce. Temperature data collected for the 2000 season revealed that there was sufficient heat accumulation during the season, under the open and light shade conditions but not under heavy shade. Successful attacks were observed on 23 of the weevil-seeded trees, which is considered to be a high level of attack (Wallace and Sullivan 1985).

The trees in this study may be too young to determine whether resistance to weevil is significantly different among the families selected for this study. The trees and families may begin to exhibit more resistance traits as they grow older and become acclimatized to the Pass Lake site.

3.5 Conclusions

The shade treatments caused the weevils to oviposit in a more dispersed pattern. However, this result did not appear to affect overall development of weevils in the light shade treatment, which had the greatest number of successful attacks. Lowered light intensity, or greater shade level also did not reduce growth of the selected spruce families. Further studies need to be undertaken to determine the role of light on oviposition behaviour of the white pine weevil, growth of spruce, and forest management implications.

CHAPTER 4

Environmental factors affecting behaviour of weevils on interior spruce clones produced by somatic embryogenesis

4.1 Introduction

Open stands of conifers are more vulnerable to attack by white pine weevil because light and temperature are increased in the open, which affects behaviour of adult insects (Sullivan 1959, 1960) and development of the brood (McMullen 1976). Previous studies (Cozens 1983; McLean 1994; Taylor *et al.* 1996) have shown that a deciduous overstorey and side-shade reduces attack by weevils on spruce. Sullivan (1961) noted that in open growing stands of white pine, weevils confined their attack to the leader and moved down the stem during the season until the distribution of punctures was relatively even throughout the length of the leader. The tendency was towards a greater proportion of oviposition punctures near the tip of the leader. However, on trees that were shaded, the distribution and frequency of oviposition punctures differed (Sullivan 1961). This is important because a dispersed pattern of oviposition lessens the chances of brood success as the likelihood of individual larvae surviving to adulthood is lessened.

This study follows from investigations undertaken in the summer of 2000 on open pollinated spruce seedlings (Chapter 3), in which it was observed that oviposition punctures made by weevils placed on interior spruce under artificial shade were lower, and less aggregated on the stem than those on open-grown trees. Using clones produced by Somatic embryogenesis (SE) (Webster *et al.* 1990) allows an investigator to eliminate population genetic variance in experimental procedures. By utilizing many trees of one clone, differences in weevil behaviour can be attributed to environmental effects such as overstorey shade.

The objectives of this study were to determine 1) if reduced light has an effect on behaviour of weevils, 2) if clones from parents previously ranked for resistance to weevils sustain

levels of attack that reflect their ranking, and 3) if bud development within clones is related to resistance to weevils. Based on the results in Chapter 3, I hypothesized that weevils placed on trees under shade would lay eggs in a dispersed pattern further down the stem than on trees in full light. Because of the more dispersed and less aggregated pattern of oviposition, weevil-larva might not be able to form feeding rings, thus fewer leaders would be killed and there would be fewer adult weevils emerging from each infested terminal.

4.2 Methodology

4.2.1 North Willow

Two SE clones of interior spruce were observed for resistance to attack by P. *strobi*. The selected clones were located in two of several trials planted in 1996 in the Sub Boreal Spruce (SBS) mk1 03, 05, 07 (moist cool, subhygric), located at North Willow, approximately 50 km east of Prince George (Latitude: 53°57' N, Longitude: 122°10' W). The trees were planted in at 2.4 m spacing in blocks of 0.20 ha (clone I-1026) and 0.15 ha (clone 107-1930). The source of clone 107-1930 originated from parents of high growth and weevil resistance rankings, while clone I-1026 originated from parents of moderate growth and weevil resistance rankings (Hawkins 1998) (Table 4.1).

Table 4.1 Growth and resistance ranking (Hawkins 1998) for SE clones from original 173 parents[1] ranked.

SE Clone	Mother – Growth	Father - Growth	Mother – Weevil Resistance	Father – Weevil Resistance
I-1026	4	78	20	97
107-1930	1	5	10	2
U284	60	36	83	15
J974	4	102	20	130
U185	60	36	83	15

[1]. There are 173 parents in the breeding population.

In 2001, 30 vigorous and healthy trees were randomly selected from each clonal block and measured for height and leader basal diameter and grouped into triplets based upon total tree height and 2000 leader growth. Each seedling in a triplet, was then randomly assigned one of three light treatments; no shade, light shade or heavy shade. Shade treatments were applied between April 30 and May 3, 2001 using 2.4 m lengths of neutral density greenhouse shade cloth (65% of light transmittance). Two, 2.4 m x 0.05 m x 0.05 m posts were driven 0.16 m into the ground 0.75 m to the east and west of each seedling. The cloth was affixed on both posts with staples, and secured to the ground with wire and metal stakes, so that 1 m of the cloth was directed to the north of the seedling and 1.4m was directed to the south of the seedling in a 45° angle. One or two layers of cloth was used to create either light shade (65% full sunlight) or heavy shade (28% full sunlight). The cloth was porous enough to allow moisture and wind through. Weevils were collected in a heavily infested stand approximately 100 km North east of Prince George on May 14 and 15th, 2001.Trees in half of the triplets in each clone and shade treatment were seeded with five weevils per tree on 15 May 2001.

Between May 12-August 29, 2001 (JD 132–241) a Campbell (Logan, Utah, U.S.A.) 21X data logger with three quantum sensors (Campbell Scientific, Inc. Edmonton, AB) and eight temperature sensors recorded light and temperature continuously on trees in the block containing SE clone 107-1930. A quantum sensor was placed at leader height affixed on a separate post beside the seedlings for each of the three light treatments. Two copper-constantin thermocouple sensors were placed on the north side of the leader just under the leader bud produced in 2000. One thermocouple was placed in the soil and the final sensor was placed in the open on the leader of a tree away from the bark, to measure air temperature. Daily treatment mean temperature above 7.2°C was determined using the formula: $\Sigma(((Tmax+Tmin)/2 + 1)-7.2)/24$. Between July 18-August 3 data lost due to equipment malfunction were interpolated based upon data from the same model data logger placed at Sinclair Mills. Lost light data were interpolated based upon data collected before and after the equipment failure (see Appendix I).

4.2.2 Upper Fraser

The second study site was located at Upper Fraser, approximately 80 km North East of Prince George (Latitude: 54°03' N, Longitude: 121°42' W) in the Sub Boreal Spruce Zone, wet, cool subvariant (SBSwk1 01). Trees at this location were planted at 2.4 m spacing in 1995 in 0.11 ha blocks. Twenty healthy and vigorous trees from each of clone U284 and J974 were randomly selected and measured for height and leader basal diameter. Clone U-284 originated from parents of moderate growth and resistance to weevils, and clone J974 originated from parents of moderate growth and low resistance ranking (Table 4.1). Trees within each clone were paired according to similar height and 2000 leader growth. Trees in half of the pairs were seeded in 2001 on 17 May, 2001 with weevils collected as above. No shade treatment was applied.

4.2.3 Assessments

The following data were collected weekly between May 14 and July 17 between 1000 and 1400 at both sites:

1. weevil behaviour: absent, feeding, mating or egg laying (oviposition sites present),
2. number of oviposition punctures on each leader as described by Wallace and Sullivan (1985),
3. distance of the furthest oviposition puncture from the top of the apical bud,
4. phenology of spruce bud burst of the leader and one lateral on the first whorl, using the classification adapted from Alfaro *et al.* (2000): (1) shiny conical – buds slightly conical with scales; (2) shiny/swollen – buds similar to the first stage but more swollen; (3) light brown/swollen – buds considerably swollen and lighter in colour than second stage; (4) columnar – shoots starting to elongate and bud scales are opaque so that green needles are visible; (5) split – shoot elongating and bud cap split; (6) brush – bud cap usually no longer present, needles appear to originate from one point; (7) feather – needle bases separate (8) growing shoot – needles widely separated out from expanding shoot.

All trees were measured for height and basal leader diameter on August 27, 2001. At this time, trees were classified as successfully attacked, based on leader-death, or not successfully attacked if the 2001 leader survived the weevil- seeding treatment. Leaders from weevil-seeded trees were removed from the tree beyond the point of initial 1999-year growth on August 29, 2001. Emergence holes were counted and each leader was dissected. Predators, parasitoids and weevil pupae were counted.

4.2.4 Upper Fraser 8 – block survey

At Upper Fraser, another clone, U185, with the same growth and weevil ranking as U284 (Table 4.1) was observed for growth and resistance to weevil. These trees were planted in eight blocks in 1995 along with seed orchard seed lot 6863 (Central Plateau) in the ratios U185:6838, 100:0, 67:33, 33:67 and 0:100, with four blocks using Peltons Nursery (PL) and four using stock form Green Timbers Nursery (GT). In early May 2001, 50 trees in each were systematically selected and tagged, and then measured for height, history of attack by weevil and attack in 2000. The blocks were re-visited in August 2001 to measure height and count current attack by weevils.

4.2.5 Statistical Analyses

All growth data were analyzed using analysis of variance, ANOVA, in SYSTAT Version 10 (SPSS, Inc. 2000). Categorical data were analyzed using Kruskal-Wallis nonparametric analysis to determine differences in shade treatments. The Kruskal-Wallis test automatically converts to the Mann-Whitney test, the non-parametric equivalent of the two-sample t-test (SPSS, Inc., 2000), when only two categories are present and was therefore used to determine differences between two shade levels or differences between clones in bud-flush. In all cases α=0.05.

4.3 Results

4.3.1 North Willow

There was no significant difference in height between clones and no interactions for all trees, but a significant difference in height between clones occurred for trees that had not been successfully attacked by the white pine weevil (Table 4.2a).

Table 4.2 Repeated measures analysis of variance results for height in 2000 and 2001, for clone, shade treatment and weevil seeded trees and their interactions at North Willow, sources identified in a) between subjects and b) within subjects.

a) Between Subjects

Source	df	MS – height All Trees	p-value All trees	df	MS – height Un-Attacked Trees	p-value Un-attacked trees
Clone	1	837.766	0.092	1	1453.192	0.022
Shade	2	233.593	0.444	2	172.177	0.514
Weevil	1	304.552	0.304	1	203.551	0.377
Clone*Shade	2	10.679	0.963	2	0.219	0.999
Clone* Weevil	1	40.745	0.706	1	51.621	0.655
Shade* Weevil	2	186.332	0.522	2	127.949	0.609
Clone*Shade* Weevil	2	785.951	0.072	2	226.732	0.418
Error	48	282.512		41	254.688	

b) Within Subjects

Source	df	MS – height All Trees	p-value All trees	df	MS – height Un-Attacked Trees	p-value Un-attacked trees
Time	1	15646.552	0.000	1	13915.713	0.000
Time * Clone	1	21.526	0.504	1	1.459	0.859
Time*Shade	2	34.949	0.485	2	70.144	0.226
Time*Weevil	1	28.808	0.440	1	19.009	0.521
Time*Clone* Shade	2	6.974	0.864	2	4.000	0.916
Time *Clone * Weevil	1	18.281	0.538	1	18.654	0.525
Time* Shade * Weevil	2	32.658	0.508	2	13.764	0.740
Time*Clone *Shade * Weevil	2	10.787	0.798	2	2.472	0.947
Error	48	47.512		41	45.445	

Time was the only significant variable for within subject testing as the trees grew in height over the summer, but time by clone was not significant, and there were no interactions (Table 4.2b). Clone I-1026 was taller than 107-1930 in 2000 and 2001, but only among trees that were not successfully attacked by the weevils (Table 4.3).

Table 4.3 Mean height (cm) for clones I-1026 and 107-1930 at North Willow; mean overall, mean of successfully attacked trees in 2001 and unsuccessfully attacked trees in 2001 for 2000 and 2001.

	I-1026						107-1930	
	2000 Mean[1]	2000 attacked[2]	2000 Not attacked[3]	2001 Mean	2001 I-1026 attacked[2]	2001 Not attacked[3]	2000 Mean[1]	2001 Mean[1]
n	30	7	23	30	7	23	30	30
Min	77.0	86.0	86.0	80.0	95.0	102.0	78.0	93.0
Max	119.0	116.0	119.0	148.0	129.0	148.0	117.0	146.0
Mean	101.0	100.2	102.3	123.2	117.2	126.7	94.4	118.2
SE	2.2	4.7	2.4	2.7	5.9	2.4	1.8	2.5

[1] Mean height of all trees in sample
[2] Mean height of trees with leaders were killed from weevils
[3] Mean height of trees with leaders that were not killed from weevils

Mean height-increment, for clone I-1026 in 2000 was 31.6 cm, compared to 24.9 cm for clone 107-1930 (Table 4.4). In 2001, clone I-1026 had the same growth increment as 107-1930 when comparing all trees.

Table 4.4 Height increment[1] (cm) for clones I-1026 and 107-1930 at North Willow.

	I-1026						107-1930	
	2000 Mean[1]	2000 attacked[2]	2000 not attacked[3]	2001 Mean[1]	2001 attacked[2]	2001 not attacked[3]	2000 Mean[1]	2001 Mean[1]
n	30	7	23	30	7	23	30	30
Min	21.0	21.0	23.0	3.0	3.0	3.0	15.0	0.0
Max	47.0	35.0	47.0	44.0	26.0	44.0	34.0	36.0
Mean	31.6	30.0	32.0	22.2	13.9	24.7	24.9	23.8
SE	1.1	2.0	1.3	1.8	2.7	2.0	1.0	1.5

[1] Mean growth increment of all trees in sample
[2] Mean growth increment of trees with leaders were killed from weevils in 2000
[3] Mean height of trees with leaders that were not killed from weevils in 2000

Basal diameter was not significantly different between clones in 2000, but was significantly different for measurements taken on the 2001 leader (Tables 4.5 & 4.6). Shade and weevil seeding did not affect 2001 leader basal diameter and there were no interactions (Table 4.6).

Table 4.5 Analysis of variance results for leader basal diameter (2000 leader) in May 2001 at North Willow.

Source	SS	df	MS	F	p-value
Clone	0.096	1	0.096	3.824	0.055
Error	1.456	58	0.025		

Table 4.6 Analysis of variance results for leader basal diameter (2001 leader) in August 2001 at North Willow

Source	SS	df	MS	F	p-value
Clone	0.164	1	0.164	7.345	0.009
Shade	0.121	2	0.061	2.718	0.076
Weevil	0.006	1	0.006	0.290	0.593
Clone*Shade	0.004	2	0.002	0.079	0.924
Clone* Weevil	0.003	1	0.003	0.137	0.713
Shade* Weevil	0.047	2	0.024	1.057	0.355
Clone* Shade* Weevil	0.006	2	0.003	0.138	0.872
Error	1.072	48	0.022		

None of the trees of clone 107-1930 seeded with weevils was attacked successfully, and no other trees within the block area, exhibited any signs of attack by weevil. There were five successful attacks on clone I-1026 of the 15 weevil-seeded trees and one of the non-seeded trees was attacked by weevils in 2001. In addition, 14 other trees from clone I-1026 that were not part of the selected sample but were within the block boundary, were also attacked by weevils, from the surrounding area or weevils that had escaped from the experiment.

No relationship was found between level of shade and number of successful attacks. However, significant relationships were found between shade and number of oviposition punctures for both clones from the fourth sampling day until the last sampling day, June 5-July 17, 2001(JD 156-198) in trees of clone I-1026 (Figure 4.1, 4.2 & 4.3).

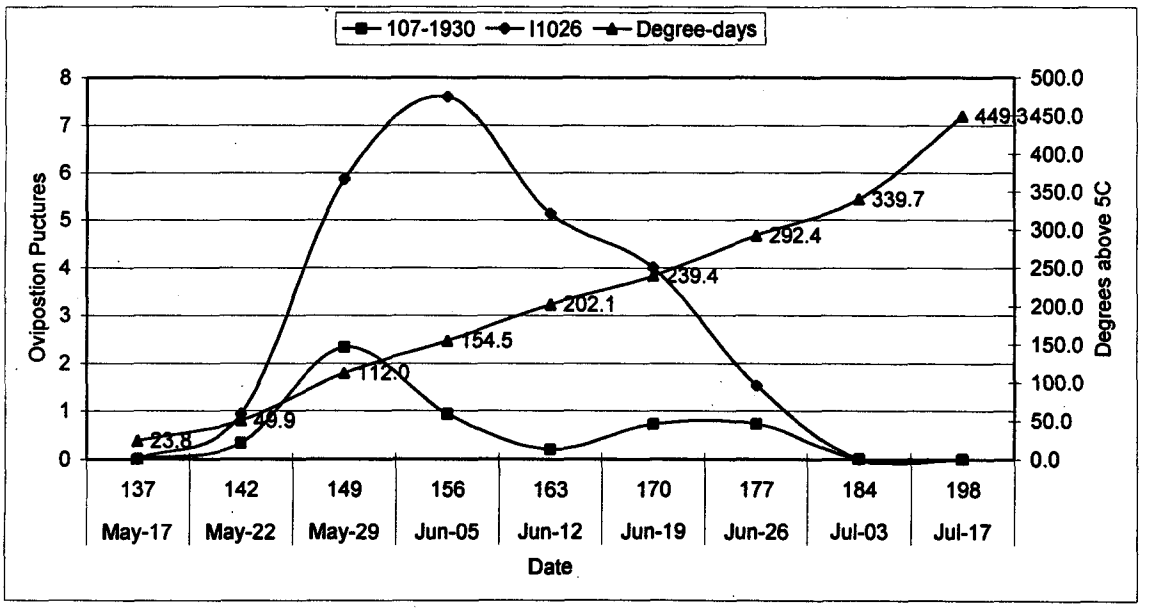


Figure 4.1 Mean oviposition punctures recorded on each sampling date for clones I-1026 and 107-1930, and accumulating degree-days above 5°C by sampling date at North Willow. May 17-July 17, 2001 (JD137-198).

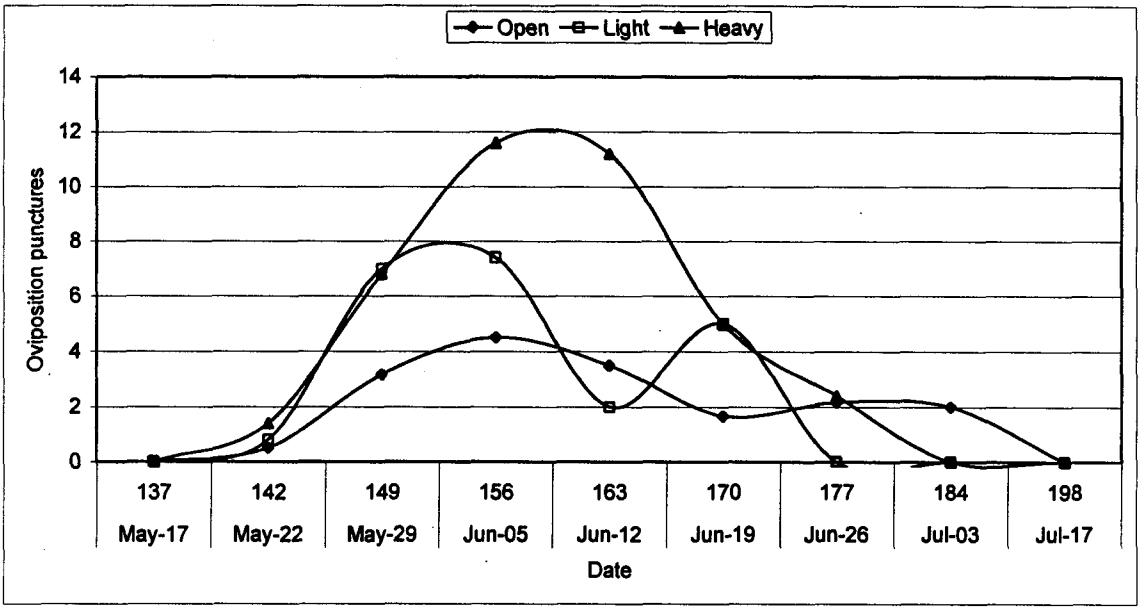


Figure 4.2 Mean oviposition punctures recorded on trees of clone I-1026 by sampling date for each shade treatment (Open, Light, Heavy) at North Willow. May 17-July 17, 2001 (JD137-198).

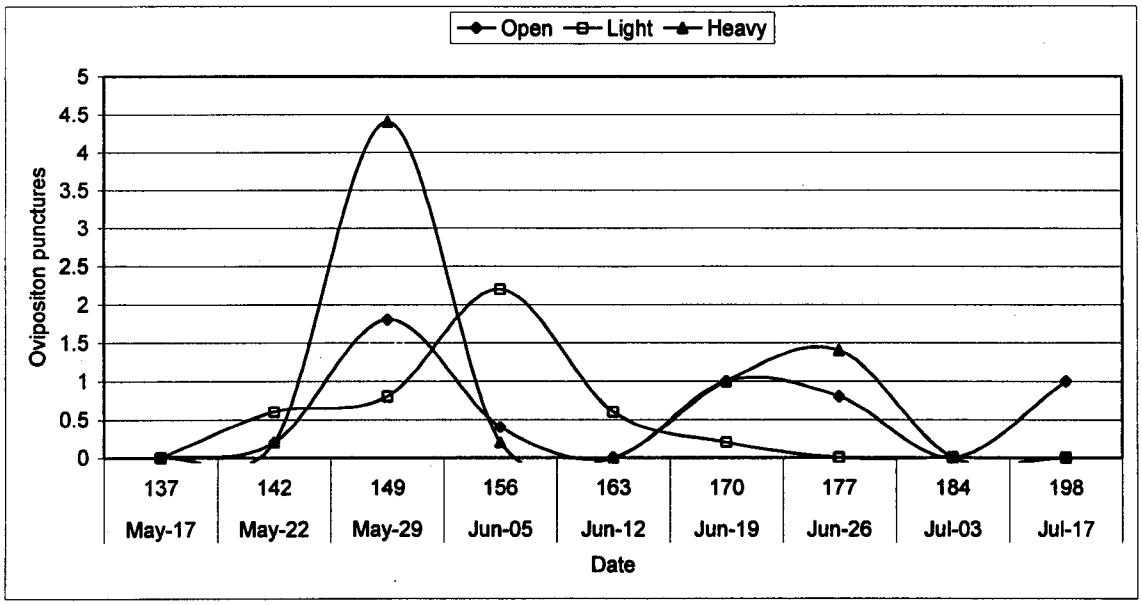


Figure 4.3. Mean oviposition punctures recorded for trees of clone 107-1930 by sampling date for each shade treatment (Open, Light, Heavy) at North Willow. May 17-July 17, 2001 (JD137-198).

A significant relationship was also found for distance of oviposition between the tip of the terminal and the lowest oviposition puncture and shade treatment, from the second sampling day May 22 (JD 142) to the last sampling day July 17 (JD 198) in clone 107-1930 (Table 4.7a).

Table 4.7 Kruskal-Wallis test for significance results between shade treatments for distance between the tip of the terminal and the lowest oviposition puncture for each sampling date for clones I-1026 and 107-1930 at North Willow a)between three shade treatments and b)-d) Mann Whitney tests between each shade treatment:

a) between three shade treatments; open, light and heavy

		I-1026		107-1930	
		Kruskal-Wallis		Kruskal-Wallis	
Sampling date (JD)	df	Test statistic	p-value	Test statistic	p-value
May 17 (137)	2	0.000	1.00	0.000	1.000
May 22 (142)	2	2.293	0.318	0.041	0.980
May 29 (149)	2	5.790	0.055	8.314	0.016
June 5 (156)	2	6.520	0.038	9.871	0.007
June 12 (163)	2	6.982	0.03	9.114	0.010
June 19 (170)	2	6.656	0.036	9.114	0.010
June 26 (177)	2	6.656	0.036	9.114	0.010
July 3 (184)	2	6.656	0.036	9.114	0.010
July 17 (198)	2	6.656	0.036	9.097	0.011

b) Mann-Whitney test for difference in distance of oviposition punctures for open and heavy shade treatments.

Sampling date (JD)	df	I-1026 Mann-Whitney U test statistic	Chi-square	p-value	107-1930 Mann-Whitney U test statistic	Chi-square	p-value
May 17 (137)	1	12.5	0.000	1.000	12.5	0.000	1.000
May 22 (142)	1	5.5	2.291	0.130	12.0	0.022	0.881
May 29 (149)	1	5.0	2.470	0.116	0.00	6.902	0.009
June 5 (156)	1	2.5	4.444	0.035	0.00	6.902	0.009
June 12 (163)	1	0.0	6.902	0.009	0.00	6.902	0.009
June 19 (170)	1	0.0	6.902	0.009	0.00	6.902	0.009
June 26 (177)	1	0.0	6.902	0.009	0.00	6.902	0.009
July 3 (184)	1	0.0	6.902	0.009	0.00	6.902	0.009
July 17 (198)	1	0.0	6.902	0.009	0.00	6.860	0.009

c) Mann-Whitney test for differences in distance of oviposition punctures for open and light shade treatments.

Sampling date (JD)	df	I-1026 Mann-Whitney U test statistic	Chi-square	p-value	107-1930 Mann-Whitney U test statistic	Chi-square	p-value
May 17 (137)	1	12.5	0.000	1.000	12.5	0.000	1.000
May 22 (142)	1	10.5	0.637	0.223	12.0	0.881	0.881
May 29 (149)	1	3.0	3.938	0.047	10.0	0.287	0.592
June 5 (156)	1	3.0	3.938	0.047	5.5	2.205	0.138
June 12 (163)	1	3.5	3.578	0.059	4.5	2.827	0.093
June 19 (170)	1	4.5	2.880	0.090	4.5	2.827	0.093
June 26 (177)	1	4.5	2.880	0.090	4.5	2.827	0.093
July 3 (184)	1	4.5	2.880	0.090	4.5	2.827	0.093
July 17 (198)	1	4.5	2.880	0.090	4.5	2.810	0.094

d) Mann-Whitney test for differences in distance of oviposition punctures for light and heavy shade treatment.

Sampling date (JD)	df	I-1026 Mann-Whitney U test statistic	Chi-square	p-value	107-1930 Mann-Whitney U test statistic	Chi-square	p-value
May 17 (137)	1	12.5	0.000	1.000	12.5	0.000	1.000
May 22 (142)	1	8.5	0.743	0.389	13.0	0.022	0.881
May 29 (149)	1	20.0	2.470	0.116	2.0	4.870	0.027
June 5 (156)	1	19.0	1.855	0.173	1.0	5.806	0.016
June 12 (163)	1	15.0	0.274	0.600	3.0	3.962	0.047
June 19 (170)	1	11.0	0.099	0.753	3.0	3.962	0.047
June 26 (177)	1	11.0	0.099	0.753	3.0	3.962	0.047
July 3 (184)	1	11.0	0.099	0.753	3.0	3.962	0.047
July 17 (198)	1	11.0	0.099	0.753	3.0	3.962	0.047

The test between open and heavy shade treatment showed the greatest level of significance in oviposition distance for all sampling dates (Table 4.7b). The effects between open and light shade treatment were only different in the third and fourth weeks (May 29 and June 5) of sampling for I-1026 but showed no difference in any dates in 107-1930 (Table 4.7c). The effects between light and heavy shade treatment were not different in any of the weeks for I-1026 but were different in all but the first weeks for 107-1930 (Table 4.7d).

The total number of oviposition punctures did not vary significantly by shade but did vary significantly by clone. Rate appeared to peak between 29 May and 12 June, 2001 when degree-days above 5°C were between 112.0 and 202.1°C. The rate of oviposition appeared different by shade treatment in clone I-1026 but not in 107-1930 (Figures 4.2 & 4.3). Rates in I-1026 appeared to be greatest for the heavy shade treatment on June 5 and June 12 (JD 156 and 163). The open treatment appeared to have the lowest overall oviposition rate for I-1026 (Figure 4.2).

There was no difference in the total number of predators and parasites found within the shade treatments in either clone. Because no leaders were killed from attacks by weevil in clone 107-1930, no adult weevils emerged from trees of this clone. Mean number of adult weevils that emerged from each leader did not vary by shade in I-1026.

Bud-development of spruce in clone I-1026 progressed faster than clone 107-1930 at North Willow (Figure 4.4).

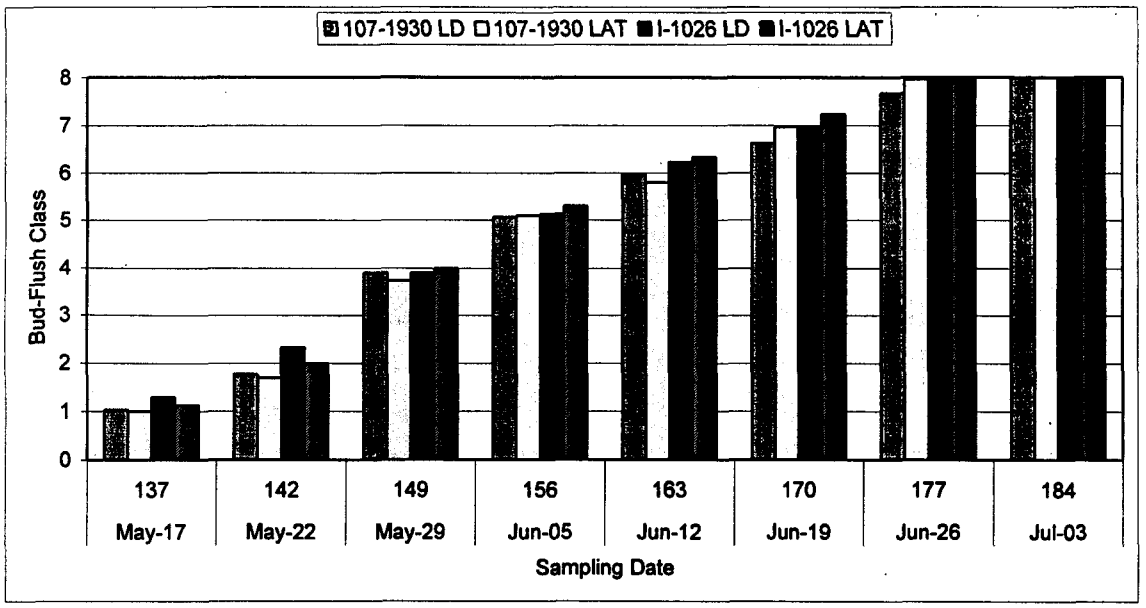


Figure 4.4 Mean Bud-flush classes of leaders (LD) and laterals (LAT) for clones I-1026 and 107-1930 at North Willow over 8 weeks: May 17-July 3 2001. Bud-flush class: (1) shiny conical (2) shiny/swollen (3) light brown/swollen (4) columnar (5) split (6) brush (7) feather (8) growing shoot. Detailed description of bud-flush classes are given in methodology section 4.3.

Lateral and terminal leader development within each clone was similar. However, bud development of the leaders was significantly different between clones in all but the third and fourth weeks of sampling (Table 4.8).

Table 4.8 Mann-Whitney results showing differences between clones I-1026 and 107-1930 at North Willow, for bud development; leaders (LD) and first whorl lateral (LAT).

	Leaders (LD)		Laterals (LAT)	
Sampling Date (JD)	Chi-Square	p-value	Chi-Square	p-value
May 17 (137)	7.552	0.006	4.214	0.040
May 22 (142)	15.233	0.000	5.659	0.017
May 29 (149)	0.094	0.759	5.671	0.017
June 5 (156)	0.439	0.508	3.687	0.055
June 12 (163)	6.017	0.014	8.866	0.003
June 19 (170)	14.450	0.000	8.536	0.003
June 26 (177)	11.800	0.001	1.000	0.317
July 3 (184)	0.000	1.000	0.000	1.000

Lateral development was significantly different from the first to third weeks, May 17-29 (JD 137-149) as well as the fifth and sixth weeks June 12-19, 2001 (JD 163-170).

Between May 12-August 29, 2001 (JD 132–241) there were 769.3, 711.0 and 675.5 degree-days above a threshold 7°C in the open, light and heavy shade treatments respectively. Average light intensity (PAR) recorded for each day under different shade treatments is seen in Figure 4.5.

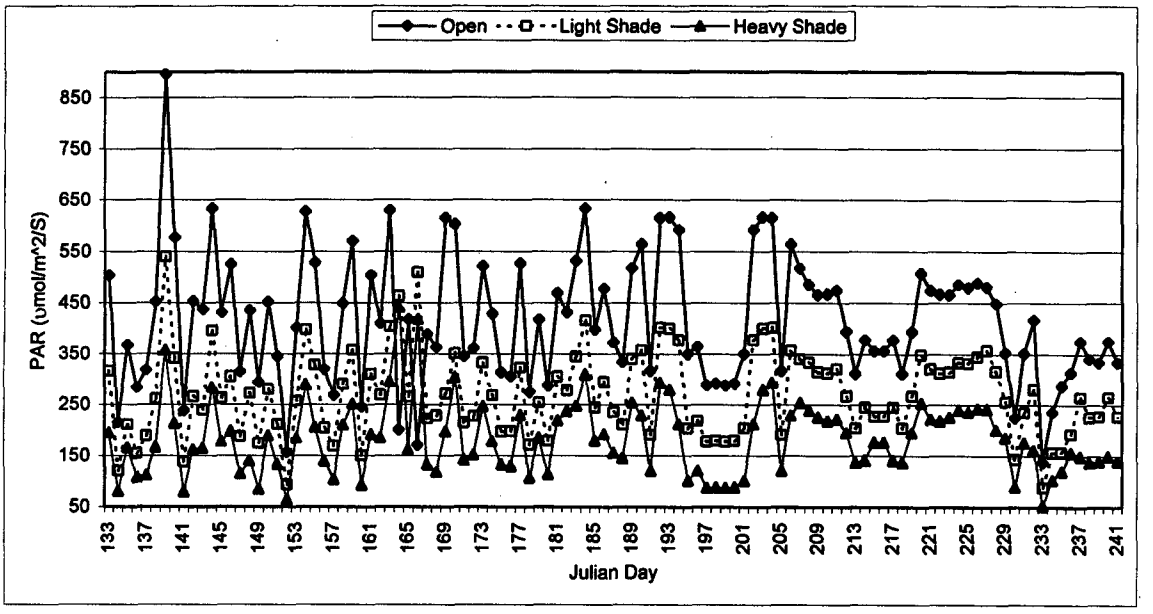


Figure 4.5 Mean daily light intensity (PAR) under shade treatments and in the open at North Willow site, 2001.

4.3.2 - Upper Fraser, Weevil-Seeded Blocks

Height differed significantly by clone at this site (Table 4.9a). Within-subject tests, with time incorporated into the model, revealed that clone was a significant factor over time (Table 4.9b).

Table 4.9 Repeated measures analysis of variance results for height in 2000 and 2001, for clone and weevil seeded trees and their interactions at Upper Fraser, a) between subjects and b) within subjects.

a) Between Subjects

Source	SS	df	MS	F	p-value
Clone	43421.880	1	43421.880	42.213	0.000
Weevil	55.444	1	55.444	0.054	0.818
Clone*Weevil	173.461	1	173.461	0.169	0.684
Error	37030.922	36	1028.637		

b) Within Subjects

Source	SS	df	MS	F	p-value
Time	26245.012	1	26245.012	527.111	0.000
Time * Clone	308.113	1	308.113	6.188	0.018
Time*Weevil	2.112	1	2.112	0.042	0.838
Time*Clone* Weevil	112.813	1	112.813	2.266	0.141
Error	1792.450	36	49.790		

There were no interactions between other independent variables. On average clone, U284 performed better in terms of height (Tables 4.10 & 4.11).

Table 4.10 Mean height (cm) for clones U284 and J974 in 2000 and 2001 at Upper Fraser.

	U284			J974		
	2000 Mean[1]	2001 Mean[1]	2001 (not-attacked)[2]	2000 Mean[1]	2001 Mean[1]	2001 (not-attacked)[2]
n	20	20	10	20	20	18
Min	132.9	163.6	181.4	93.4	116.7	116.7
Max	205.4	243.3	242.5	168.0	214.0	214.0
Mean	162.1	202.2	203.3	119.4	151.7	152.0
SE	5.1	5.4	6.1	19.5	23.8	25.1

[1] Mean height of all trees sampled

[2] Mean height of trees with leaders that were not killed from weevils

Table 4.11 Height increment (cm) for clones U284 and J974 in 2000 and 2001 at Upper Fraser.

	U284			J974		
	2000 Mean[1]	2001 Mean[1]	2001 (not-attacked)[2]	2000 Mean[1]	2001 Mean[1]	2001 (not-attacked)[2]
n	20	20	10	20	20	18
Min	26.0	15.0	29.0	21.1	19.0	19.0
Max	64.2	56.0	56.0	47.0	46.0	46.0
Mean	43.3	40.2	46.4	32.4	32.3	32.6
SE	0.5	0.6	1.0	1.4	1.7	1.8

[1] Mean height increment of all trees sampled

[2] Mean height increment of trees with leaders that were not killed from weevils

Leader basal diameter did not vary significantly between clones for the 2000 leader-growth. There was, however, a significant difference between basal diameters in 2001 (Table 4.12). The weevil-seeding treatment did not affect diameter growth, nor was there an interaction between weevil-seeding and clone. This indicated that differences in the basal-girth of the 2001 leader between clone, were present due to selection of the trees, or some other extraneous variable, and not due to weevil-seeding.

Table 4.12 Analysis of variances results for leader basal diameter (2000 leader) in May 2001 and leader basal diameter in August 2001 (2001) leader at the Upper Fraser.

	Source	SS	df	MS	F	p-value
2000 Leader	Clone	0.014	1	0.014	1.052	0.312
	Weevil	0.003	1	0.003	0.211	0.649
	Clone* Weevil	0.020	1	0.020	1.476	0.232
	Error		36	0.014		
2001 Leader	Clone	0.089	1	0.089	5.352	0.0270
	Weevil	0.001	1	0.001	0.066	0.799
	Clone* Weevil	0.056	1	0.056	3.326	0.076
	Error	0.601	36	0.017		

Clone U284 sustained more successful attacks than J974; with 7 attacks on U284 and 3 on J974 respectively. Three un-seeded control trees were also attacked successfully in U284. Five additional trees, not within the selected sample were also attacked successfully within the block of clone U284 and three additional trees not within the selected sample were attacked in the J974 block. Mean number of oviposition punctures also differed between each clone (Table 4.13).

Table 4.13 Mean number of oviposition punctures for clones U284 and J974 at Upper Fraser.

	U284	J974
n	10	10
Min	1.0	0.0
Max	107.0	30.0
Mean	52.8	5.6
SE	12.9	3.6

The rate of oviposition between the two clones at this site appeared different (Figure 4.7).

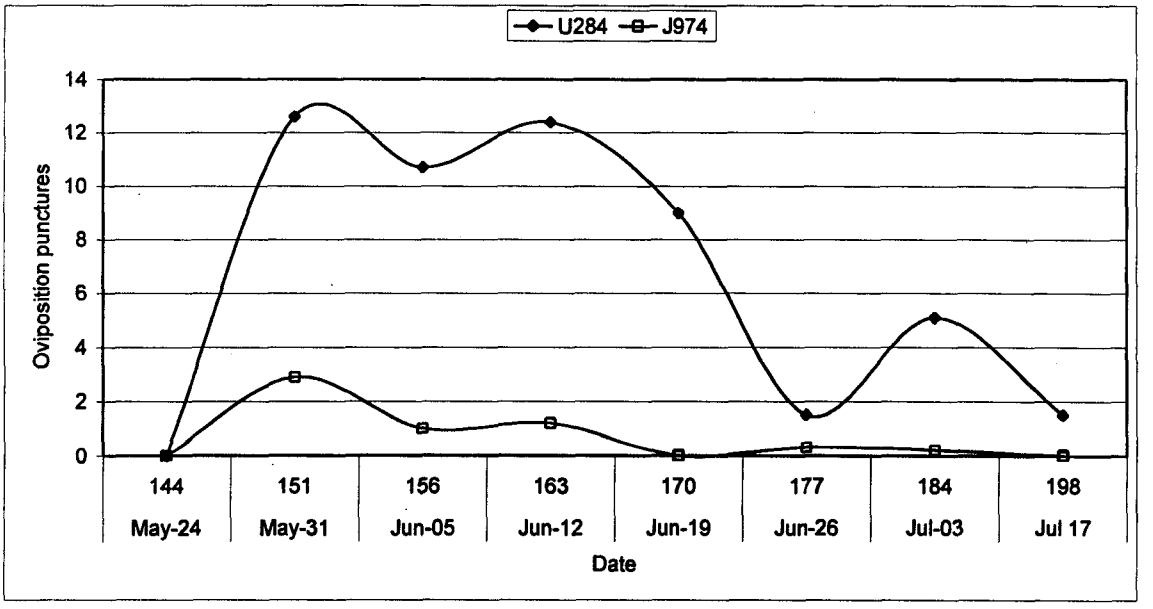


Figure 4.6 Mean oviposition punctures by sampling date for Clones U284 and J974 at Upper Fraser, calculated by mean difference in weekly oviposition punctures per sampling date, May 24-July 3, 2001 (JD144-198).

Total number of parasites and predators differed significantly by clone (Table 4.14).

Table 4.14 Mean number of predators and parasites and weevils emerged from U284 at Upper Fraser.

	U 284		J974	
	Predators & Parasites	Weevils Emerged	Predators & Parasites	Weevils Emerged
n	10	10	10	10
Min	0.0	0.0	0.0	0.0
Max	32.0	6.0	5.0	0.0
Mean	3.4	1.9	1.0	0.0
SE	2.53	0.61	5.88	0.00

No adult weevils emerged from clone J974 even though attack by weevils resulted in three dead leaders in this clone.

Bud-development between clone differed significantly between the first and fourth week of sampling (Table 4.15), but lateral bud development did not differ significantly between clones on

any of the sampling dates. For most sampling dates, leader and lateral development within each clone was similar (Figure 4.7).

Table 4.15 Differences between clones J974 and U284 for bud development, leaders (LD) and first whorl lateral (LAT) using Mann-Whitney non-parametric analysis.

	Sampling Date (JD)	Leaders (LD)		Lateral (LAT)	
Week		Chi-Square	p-value	Chi-Square	p-value
1	May 24 (144)	14.832	0.000	0.223	0.637
2	May 31 (151)	0.219	0.639	0.205	0.651
3	June 5 (156)	3.016	0.082	0.193	0.661
4	June 12 (163)	4.016	0.045	1.013	0.314
5	June 19 (170)	2.773	0.096	1.334	0.248
6	June 26 (177)	1.000	0.317	1.000	0.317
7	July 3 (184)	0.000	1.000	0.000	1.000
8	July 17 (198)	0.000	1.000	0.000	1.000

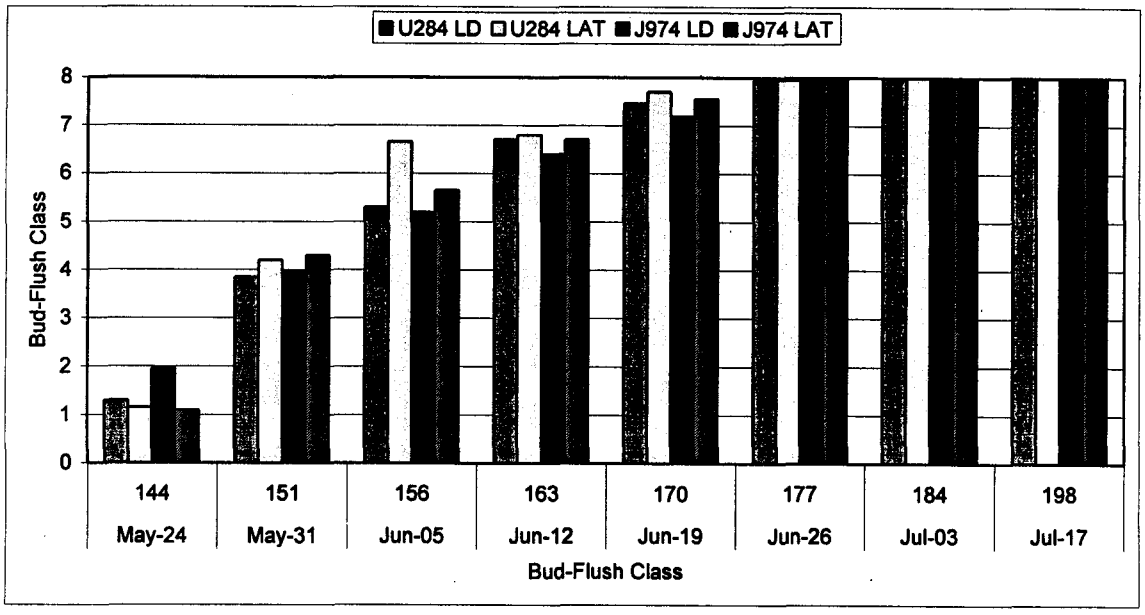


Figure 4.7. Mean Bud-flush classes of leaders (LD) and laterals (LAT) for clones U284 and J974 at North Willow over 8 weeks: May 24-July 17 2001. Bud-flush class: (1) shiny conical (2) shiny/swollen (3) light brown/swollen (4) columnar (5) split (6) brush (7) feather (8) growing shoot. Detailed description of bud-flush classes are given in methodology section 4.3.

4.3.3 Results -Upper Fraser, 8-block survey

Height differed significantly in 2000 and 2001 by nursery and for all mixes of clone and seedlot sampled (Tables 4.16 & 4.17).

Table 4.16 Height (cm ±SE) in 2000 and 2001, height increment (cm ±SE) 2001 and percentage of trees attacked by weevils historically, in 2000 and in 2001 for Upper Fraser blocks; Peltons Nursery (PL) and Green Timbers Nursery (GT) using clone U185 and seedlot 6864.

	Height					
Nursery (Percent of clone U185)[1]	2000	2001	Increment 2001	% Attack History	% Attack 2000	% Attack 2001
GT-1 (100%)	71.0 (3.2)	97.3 (3.8)	25.8 (1.6)	8	2	2
GT-2 (67%)	85.4 (4.0)	112.0 (5.1)	25.7 (2.6)	16	8	10
GT-3 (33%)	96.6 (3.6)	126.9 (4.5)	30.3 (1.9)	16	8	8
GT-4 (0%)	105.3 (4.3)	135.2 (5.2)	30.0 (3.2)	20	8	4
PL-1 (100%)	86.5 (3.5)	120.2 (5.0)	33.2 (2.9)	2	2	4
PL-2 (67%)	89.5 (3.4)	121.5 (4.3)	32.0 (3.0)	12	4	8
PL-3 (33%)	101.3 (5.4)	147.7 (9.2)	43.8 (6.9)	24	8	4
PL-4 (0%)	123.1 (3.3)	158.7 (3.1)	35.6 (4.0)	40	38	4

[1] Blocks were planted by percent of clone U185 in 100, 67, 33 and 0 % clone with remaining portion planted with trees from seedlot 6864. Clones and seedlings from seed-lot stock were inter-mixed in blocks that were not 0 or 100%.

Table 4.17. Repeated measures analysis of variance results for height in 2000 and 2001, for nursery, percent clone of U185 and their interactions at Upper Fraser, a) between subjects and b) within subjects.

a) Between subjects

	Sum-of-Squares	df	Mean-Square	F-ratio	p-value
Nursery	44631.491	1	44631.491	24.147	0.000
% Clone	158696.744	3	52898.915	28.620	0.000
Nursery * % Clone	6219.461	3	2073.154	1.122	0.340
Error	711609.235	385	1848.336		

b) Within subjects

	Sum-of-Squares	df	Mean-Square	F-ratio	p-value
Time	201697.716	1	201697.716	693.911	0.000
Time* Nursery	3296.964	1	3296.964	11.343	0.001
Time* % Clone	2051.620	3	683.873	2.353	0.072
Time* Nursery * % Clone	469.494	3	156.498	0.538	0.656
Error	111907.169	385	290.668		

There was a significant difference in height-growth between the two nurseries (Table 4.17a) with Peltons having a greater height increment (Table 4.16). Within-subject testing revealed only nursery to be significantly different over time, while percent clone was not (Table 4.17b). However, height increment did not vary significantly between the clone and seedlot planting mixtures. Rates of attack differed significantly by percentage of clone in blocks planted with trees from Peltons but not in the Green Timbers blocks in 2000 (Table 4.17). Evidence of attack-history differed between the percentage of clone with the greatest and least rates of attack in the 0% and 100% clonal blocks respectively.

4.4 Discussion

4.4.1 Growth of Spruce and Incidence of Attack by Weevils

Clone I-1026 had a larger height increment than 107-1930, which was not expected according to prior rankings for growth (Table 4.1). At Upper Fraser, clone U284 had a larger height increment than J974 even though both clones were ranked similarly for growth. The clones that grew fastest at both sites had the highest levels of weevil-attack. Clone I-1026 was ranked lower in terms of weevil resistance than 107-1930, and appeared to perform accordingly, as no trees from clone 107-1930 were attacked. However, within the entire breeding population (173) both clones chosen at North Willow were ranked relatively high for weevil resistance (Table 4.1).

The ability of clone 107-1930 to resist attack by weevil may override its open-growing locale. The lowest ranked clones in this study, U185 and U284 performed poorly in terms of resistance to weevils. Clone U284 at Upper Fraser sustained the greatest number of attacks on trees that had been weevil-seeded. However, I-1026, at North Willow, had the greatest number of attacks by weevils on trees that were not seeded. This could be due to the adjacent spruce progeny-trial, which appeared to have a high rate of attack within the block. Clone J974, which had a relatively low paternal ranking for resistance to weevils, did not have a high rate of attack.

The 8-block trial at Upper Fraser, with varying mixtures of seedlot trees and cloned trees, were significantly different in height and growth. Clone U185 performed poorly, in terms of growth, in comparison to the seedlot stock. This was surprising as U284, which had the same resistance-ranking as U185, grew faster than J974, even though both trials were located within 150 m. However, differences in site-series may have been present between the two trials.

4.4.2 Artificial Shade and Overstorey

No significant relationship was found between leaders killed by weevils and shade treatments at North Willow. Several reasons may account for this finding. Sullivan (1961) noted that one of the main differences between shaded and open stems was that shaded stems were

thinner. In my experiment at North Willows, the trees had been growing in the open since planting and had not developed thinner leaders on which the weevils were placed. Any altered properties of the leader, either physical or chemical, resulting from the shade treatments would not be seen until at least the following season. The weevils would therefore not respond to the leader in the same manner as if it had been growing in reduced light conditions over several years.

At North Willow, a significant relationship was found with the distance of oviposition and shade treatment, the greatest dispersal of oviposition punctures were on trees under shade treatments compared to the open. This is commensurate with findings in the Pass Lake study (Chapter 3). This evidence appears to support findings by Sullivan (1961). However, successful attack was not related to shade treatment. This was shown by examining the differences in oviposition punctures by sampling date under each shade treatment. The number of oviposition punctures was not reduced by the shade treatments. In addition, the number of adult weevils emerging by shade treatment did not vary, which would be expected if shade treatment had an effect on brood development. Sullivan (1961) also observed that the weevils under shade fed and oviposited beyond the terminal leader, but in my experiments weevils did not oviposit beyond the leader.

The variable findings for the shade experiments may be a result of many factors within the experimental design itself. As in Sullivan's (1961) study, the weevils were placed on the leaders and did not choose the host themselves. However, the neutral density shade cloth does not have the same physical properties as a deciduous canopy which would alter the spectral properties beneath it. The shade cloth merely reduces the intensity of light, whereas a deciduous canopy alters both intensity and quality of light. I hypothesize that if the experiment were to be modified using either a natural canopy of deciduous trees, or material with similar spectral properties, more varied and conclusive results regarding oviposition behaviour of weevils would be found.

Another source of the conflicting results may be that the weevils were not caged, as in Sullivan's (1961) trials, and therefore were free to leave undesirable trees, be preyed on, or blown

away in extremely windy conditions. It is debatable if Sullivan's (1961) weevils would have stayed on the trees and fed in this manner if they were not caged on the tree itself. Other sources confounding the results may arise from the physical properties of the shade cloth. Even though the cloth was porous, temperatures were not greatly reduced under the shade treatments, as would be the effect under some types of natural canopy. During the early oviposition period in May, average daily temperature was sometimes greater under the shade. This could be due to the insulating effect of the dark shade cloth which kept temperatures warmer during the night, resulting in a higher average over the 24-hour period.

4.4.3 Bud-development of Spruce

Hulme (1995) noticed that in Sitka spruce clones, generally the least damaged trees, by *P. strobi*, initiated apical bud development earlier in the season relative to susceptible clones. Alfaro *et al.* (2000) found that budburst development was under strong genetic control and that on average spruce families with resistance to attack by weevil initiated and maintained a faster rate of bud development than families from susceptible parents. However, there was considerable overlap between resistant and non-resistant families (Alfaro *et al.* 2000). At North Willow, trees from clone I-1026, which had the lower maternal and paternal rankings for resistance to weevils, developed sooner than trees from clone 107-1930, but had a higher incidence of attack from weevils. This supports the general findings of Hulme (1995) and Alfaro *et al.* (2000) that phenology and resistance of spruce are not always related. There may be species differences between Sitka and interior spruce, as differences were seen between lag-time between leader and lateral bud-break. Alfaro *et al.* (2000) found that lateral buds in Sitka spruce develop sooner than leaders. At North Willow, lateral bud-development in interior spruce clones lagged behind leader bud-development for the first few weeks (Figure 4.4) and then caught up to leader phenology. However, this may be due the effects of water availability, or lower spring temperatures, rather than a specific species difference between the spruces.

At Upper Fraser, the leaders and lateral from J974 developed sooner, and had fewer successful attack by weevils than U284. These clones both had moderate resistance rankings and it is therefore difficult to delineate whether or not the more resistant clone developed sooner. The reason for the difference between I-1026 and 107-1930 may be a consequence of the unknown basis for the original ranking of resistance to weevils. Resistance, is based upon many traits and different mechanisms, which may or may not be related to bud phenology (Kiss and Yanchuk 1991; Alfaro *et al.* 2000). Planting location may also play a role, as the site at Upper Fraser appeared to be richer and more productive, while the site at North Willow appeared less productive. Budburst phenology is also influenced by heat, both air and soil, and water availability (Dormling *et al.* 1968).

Although bud-burst phenology did not correlate with resistance, the rankings for resistance did follow closely with their original status; U284, was the clone with the most numerous leaders killed due to attack by weevils followed by I-1026 and then J974. Clone 107-1930 had no incidence of attack by weevils in the study as well as no incidence of attack outside of the randomly selected trees.

4.5 Conclusions

There appeared to be a strong genetic component for resistance to weevil in clone 107-1930, but not in the other clones. It is unknown what the trait, or traits, of resistance were functional in clone 107-1930. Bud-development did not appear to relate to any resistance mechanism in the clones studied. Further studies, utilizing a larger number of clones, need to be done to determine if mechanisms relating to bud-flush, are shown in interior spruce that influence resistance to weevils. Shade may play a role in behaviour of weevils, but the results from this study are inconclusive. Further studies using shade, which simulate changes in light quality, need to be done on interior spruce in order to determine what role light plays in influencing the oviposition-behaviour of *Pissodes strobi*.

CHAPTER 5

Conclusions and Recommendations

5.1 Summary and integration of major findings

The overall objective of this study was to determine if shade, or lowered light levels, created by natural or artificial treatments, reduced rates of attack by the white pine weevil on interior spruce trees. Data collected at Sinclair Mills, where natural overstorey created by paper birch lowered rates of attack by the weevil in a 13-year old spruce plantation, supported previous studies regarding such mitigating effects. However, this was not found in the studies using artificial treatments to create shade over young spruce seedlings. The latter were used in the spruce-family trial at Pass Lake in the summer of 2000 and the spruce clonal studies at North Willow in 2001. The main difference, between the artificial and natural shade, was the effect on the quality of light transmitted. The spectral distribution was altered under natural conditions, but remained unchanged under artificial conditions. Near infrared wavelengths became more prominent under birch trees, while shorter wavelengths were reduced.

At Sinclair Mills, the primary objectives were to 1) quantify growth of spruce and rates of attack by weevils in the control and open stands four years after vegetation removal with glyphosate, and 2) follow attack-rates by weevils over the two-year study period. Percentage of attack by weevils was significantly less on interior spruce and height-growth of spruce was significantly better in the control area compared to the open area, previously treated with herbicide.

Secondary objectives at Sinclair Mills were to quantify the effects of birch overstorey on open and shaded spruce trees as differences in light and temperature. The shape of the crown in paper birch allowed substantial amounts of light through the canopy. Light was reduced on average 23% in the control area after completion of deciduous bud-break. However, because paper birch within the plantation was not uniformly dispersed, percentage of full light varied greatly. Light

quality was also different under the birch canopy compared to the open. Temperature was different between open and shaded trees but average daily air temperature at the leader did not differ greatly between shaded and open trees. This however, may be a limitation of the experimental design and placement of the temperature sensors. Birch densities in the control ranged from 700 to 3500 sph and maximum total (spruce plus birch) densities were 3465 sph.

Stands in the control area would not meet current free-growing definitions due to competition and the treated area would not be classed as free- growing due to attack by weevil. Competition at the observed densities did not reduce growth of spruce and the overstorey appeared to reduce levels of attack by white pine weevil. Others, (Simard and Hannam 2000) have found that paper birch self-thins rapidly when growing in mixed stands. Initial densities of paper birch of up to 60,000 sph were reduced to an average of 6000 sph by age 10, and 1500 sph by 15 yrs in the ICH Biogeoclimatic zone (Simard and Vyse 1994). Upper and lower bounds of birch stocking for enhancing spruce growth in the SBS have yet to be delineated. The growing environment for spruce, created by the paper birch overstorey probably played a role in reducing incidence of attack by weevils in the control area. However, further studies are necessary to determine specific mechanisms which result in reduced incidence of attack on spruce under a birch canopy.

The study at Sinclair Mills confirms previous hypotheses that predict the removal of broadleaf competition, to enhance conifer growth, may result in increased rates of attack by weevils (Lanier 1983; Alfaro *et al.* 1994). When the deciduous competitor species were removed, incidence of attack by weevils was much higher in the open, treated area. It is hypothesized that the re-growth of paper birch into the plantation, after sheep grazing to remove vegetation, had a negative effect on the already present population of weevils. Because glyphosate targets the shikimic acid pathway in plants (Stasiak *et al.* 1992) it is highly unlikely that the herbicide directly affected weevil physiology, and the influence on population-growth was likely due to abundance of food, breeding sites, and microclimate.

Both treated and untreated stands had substantial evidence of previous attack, yet populations of weevils in each area must have diverged after treatment. The primary variable affecting this change was the presence of birch which created overstorey shade. The lack of birch, or other deciduous species, in the treated area created favourable habitat for the weevils in several ways. Snow in the treated area melted sooner than in the control area, allowing ground temperatures to warm the sites where weevils overwinter. The absence of birch in the area treated with herbicide would have allowed weevils a clear view of the leader. Shaded spruce leaders under the birch canopy may have had thinner bark or increased resin canal density, a primary defence in spruce against weevil (Tomlin and Borden 1997b).

The main objectives for the studies at Pass Lake and North Willow, were to determine the effects of artificial shade on initial attack by weevils placed on planted spruce seedlings at the tree, family and clone level. It was thought that weevils under shade, without having to find a host tree, would oviposit at a normal rate and pattern unimpeded by reduced light intensity. However, the shade treatments at Pass Lake and North Willow caused the weevils to oviposit in a dispersed pattern. This result did not appear to affect overall development of insects in the light shade treatment under which the greatest number of successful attacks occurred. Lowered light intensity, or greater shade level also did not reduce growth of the selected families of spruce, which is consistent with findings from Logan (1969).

A detailed data collection at North Willow revealed that although the shade treatment caused a change in the dispersion of oviposition punctures there was no impact on the number per tree.

5.2 Experimental benefits, design and liabilities

Temperature is inextricably linked to the intensity of light in field situations, and therefore cannot be isolated except under laboratory or greenhouse conditions. This was the case for all studies undertaken within this thesis. Shade created by natural or artificial means ultimately

reduces overall temperature accumulation. Therefore, only inferences are made regarding the affect of light in a natural setting to the effects of successful attack by the white pine weevil. Mean daily temperature, taken at the leader, did not differ greatly between open and shaded trees in Sinclair Mills. Light samples taken at the leader continuously over the season were much different under shaded *versus* open trees. This suggests that light and temperature may be linked more loosely in a natural setting, compared to laboratory conditions.

5.2.1 Sinclair Mills

Estimates of tree-form between trees from the treated and control areas at Sinclair Mills were markedly different. These estimates of damage range from severe to moderate attack, may however be conservative. Estimates of minor damage were based upon defects occurring above 2 m. Damage such as a fork or severe crook, below 2 m was given the categorical ranking of severe damage. However, an improvement to this ranking system should incorporate a larger length of clear bole and implement damage rankings above and below 2.54 or 5.08 m (first two logs), as it more closely represents the length of saw timber used in this area. A larger sample size of leaders may have been more useful to examine parasite populations, as no significance was found when comparing weevil-infested leaders from open and shaded trees. A data logger set up in the open, treated area would have been useful to account for temperature differences between the two sites. In addition, this un-replicated study is limited as plot-replicates controlled for variation in sampling but not the effects of treatment.

5.2.2 Pass Lake

Using artificial shade allowed the level, or intensity of light to be controlled and replicated many times. Use of pedigreed families introduced known levels of resistance. Weevils were not sexed before seeding which may have caused variation in success of attack, but the probability of having all males or females on a single tree is only 0.03125, as the sex ratio of *P. strobi* is

approximately 50:50. Shade treatments that altered the quality of light as well as the intensity would aid in determining how light affects oviposition behaviour of weevils on interior spruce. A follow up study over several years would be useful to determine if traits within families for growth and resistance are expressed when trees are older.

5.2.3 North Willow

Using SE clones of spruce at North Willow resulted in no variance in genetic make-up between individual trees of the same clone. Therefore, all responses by weevils on the trees should be attributable to environment. However, the choice of SE clones was limited because only clones produced in large numbers were available for deployment (Hawkins, Pers. Comm. 2000). The design was limited because only two clones were tested with the shade treatments and only one clone, I-1026, was attacked successfully by weevils. In addition weevils from the endemic population attacked trees not seeded in the experiment. The design of the shade structures may have hindered movement of the insects by trapping them on the trees under the shade structures. This study would be of more relevance if conducted over several seasons. Shade would need to be installed at least 2 years before the experiment so that trees could adopt characteristics of spruce-trees growing under natural overstorey. Traits, associated with resistance not expressed during the trial could be expressed at an older age, and therefore a follow up study of this site is justified.

5.3 Recommendations

In areas where attack by weevil rates are high, care should be taken when implementing vegetation management procedures. Birch at levels equal to or less than that found in Sinclair Mills, at a maximum of 3500 sph (spruce and birch), should probably be left until trees are of substantial height to ensure clear, straight saw quality timber in the SBS vk. This would need to be defined for other subzones in the SBS that are have a high hazard rating for white pine weevil. Free-growing regulations may need to be revised, as limits for deciduous species may be too low

for spruce plantations at risk of attack by weevils. A results-based Forest Practices Code would be useful for managing stands with high levels of attack. Studies also need to be done on the relationship between light and aspen, as this is a more prominent deciduous species in the Sub Boreal Spruce Zone (Peterson and Peterson 1995). In addition, aspen has a different crown structure and area than paper birch. Aspen, present at approximately 1000 sph creates 50% full light (Comeau 2001) while the study at Sinclair Mills showed that twice as many sph of birch resulted in 77% full light.

The use of families, or clones, known to show resistance to attack by white pine weevil may be beneficial for deployment in high hazard areas of the SBS. The families of spruce at Pass Lake should be revisited in a follow up study to determine if resistance in spruce, to attack by weevils, is expressed as trees age. Clones of spruce may also prove to be useful in an operational setting. Clone 107-1930, would be of interest for further testing as no individual trees at the site were attacked by either seeded or endemic weevils. Deployment of clonal mixtures, rather than monoclonal blocks, within a plantation may reduce selective pressure on populations of weevil.

The complexity, dynamics and economic importance of spruce, and the white pine weevil and deciduous angiosperm trees in the SBS warrants further study if these stands are to be managed as a sustainable resource. In the future, commercial productivity may be maximized when, broad-leaf vegetation is incorporated and managed as a main component within the stand.

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APPENDIX I

Campbell 21X Micrologger programs

A. 21x Micrologger program for Sinclair Mills 2001

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;{21X}

*Table 1 Program
  01: 10      Execution Interval (seconds) ;

1: Internal Temperature (P17)
  1: 12      Loc [ TC_ref    ]

2: Thermocouple Temp (SE) (P13)
  1: 8       Reps
  2: 2       15 mV Slow Range
  3: 1       SE Channel
  4: 1       Type T (Copper-Constantan)
  5: 12      Ref Temp (Deg. C) Loc [ TC_ref
]
  6: 1       Loc [ Temp_1    ]
  7: 1.0     Mult
  8: 0.0     Offset

3: Volt (Diff) (P2)
  1: 1       Reps
  2: 2       15 mV Slow Range
  3: 5       DIFF Channel
  4: 9       Loc [ Q10183    ]
  5: 255.75  Mult
  6: 0.0     Offset

4: Volt (Diff) (P2)
  1: 1       Reps
  2: 2       15 mV Slow Range
  3: 6       DIFF Channel
  4: 10      Loc [ Q10534    ]
  5: 303.95  Mult
  6: 0.0     Offset

5: Volt (Diff) (P2)
  1: 1       Reps
  2: 2       15 mV Slow Range
  3: 7       DIFF Channel
  4: 11      Loc [ Q16883    ]
  5: 344.83  Mult
  6: 0.0     Offset

6: Z=F (P30)
  1: 5019    F
  2: 13      Z Loc [ LogID    ]

7: Batt Voltage (P10)
  1: 14      Loc [ Battery   ]

8: If time is (P92)
  1: 0       Minutes into a
  2: 60      Minute Interval
  3: 10      Set Output Flag High

9: Real Time (P77)
  1: 1220    Year,Day,Hour/Minute (midnight
= 2400)

10: Sample (P70)
  1: 1       Reps
  2: 13      Loc [ LogID    ]

11: Average (P71)
  1: 11      Reps
  2: 1       Loc [ Temp_1    ]

12: Maximum (P73)
  1: 8       Reps
  2: 10      Value with Hr-Min
  3: 1       Loc [ Temp_1    ]

13: Minimum (P74)
  1: 8       Reps
  2: 10      Value with Hr-Min
  3: 1       Loc [ Temp_1    ]

14: Serial Out (P96)
  1: 30      SM192/SM716/CSM1

*Table 2 Program
  02: 0.0000    Execution Interval (seconds)

*Table 3 Subroutines

End Program

-Input Locations-
1 Temp_1    1 3 1
2 Temp_2    1 3 1
```

3 Temp_3 1 3 1
4 Temp_4 9 3 1
5 Temp_5 9 3 1
6 Temp_6 9 3 1
7 Temp_7 9 3 1
8 Temp_8 17 3 1
9 Q10183 5 1 1
10 Q10534 1 1 1
11 Q16883 1 1 1
12 TC_ref 1 1 1
13 LogID 1 1 1
14 Battery 1 0 1
15 _____ 0 0 0
16 _____ 0 0 0
17 _____ 0 0 0
18 _____ 0 0 0
19 _____ 0 0 0
20 _____ 0 0 0
21 _____ 0 0 0
22 _____ 0 0 0
23 _____ 0 0 0
24 _____ 0 0 0
25 _____ 0 0 0
26 _____ 0 0 0
27 _____ 0 0 0
28 _____ 0 0 0
-Program Security-
0
0000
0000

Final Storage Label File for: SINCLR01.CSI
Date: 4/23/2001
Time: 10:56:16

108 Output_Table 60.00 Min
1 108 L
2 Year_RTM L
3 Day_RTM L
4 Hour_Minute_RTM L
5 LogID L
6 Temp_1_AVG L
7 Temp_2_AVG L
8 Temp_3_AVG L
9 Temp_4_AVG L
10 Temp_5_AVG L
11 Temp_6_AVG L
12 Temp_7_AVG L
13 Temp_8_AVG L
14 Q10183_AVG L
15 Q10534_AVG L
16 Q16883_AVG L
17 Temp_1_MAX L
18 Temp_1_Hr_Min_MAX L
19 Temp_2_MAX L
20 Temp_2_Hr_Min_MAX L
21 Temp_3_MAX L
22 Temp_3_Hr_Min_MAX L
23 Temp_4_MAX L
24 Temp_4_Hr_Min_MAX L
25 Temp_5_MAX L
26 Temp_5_Hr_Min_MAX L
27 Temp_6_MAX L
28 Temp_6_Hr_Min_MAX L
29 Temp_7_MAX L
30 Temp_7_Hr_Min_MAX L
31 Temp_8_MAX L
32 Temp_8_Hr_Min_MAX L
33 Temp_1_MIN L
34 Temp_1_Hr_Min_MIN L
35 Temp_2_MIN L
36 Temp_2_Hr_Min_MIN L
37 Temp_3_MIN L
38 Temp_3_Hr_Min_MIN L
39 Temp_4_MIN L
40 Temp_4_Hr_Min_MIN L
41 Temp_5_MIN L
42 Temp_5_Hr_Min_MIN L
43 Temp_6_MIN L
44 Temp_6_Hr_Min_MIN L
45 Temp_7_MIN L
46 Temp_7_Hr_Min_MIN L
47 Temp_8_MIN L
48 Temp_8_Hr_Min_MIN L

Estimated Total Final Storage Locations used per day 1152.0

Program Trace Information File for:
SINCLR01.CSI
Date: 4/23/2001
Time: 10:56:16

T = Program Table Number
N = Sequential Program Instruction Location Number
Instruction = Instruction Number and Name

Inst ExTm = Individual Instruction Execution Time

Block ExTm = Cumulative Execution Time for program block,
i.e., subroutine
Prog ExTm = Cumulative Total Program Execution Time

Output Flag High

T|N|Instruction	Inst ExTm (msec)	Block ExTm (msec)	Prog ExTm (msec)	Inst ExTm (msec)	Block ExTm (msec)	Prog ExTm (msec)
1|1|17 Internal Temperature	14.0	14.0	14.0	14.0	14.0	14.0
1|2|13 Thermocouple Temp (SE)	226.4	240.4	240.4	226.4	240.4	240.4
1|3|2 Volt (Diff)	74.9	315.3	315.3	74.9	315.3	315.3
1|4|2 Volt (Diff)	74.9	390.2	390.2	74.9	390.2	390.2
1|5|2 Volt (Diff)	74.9	465.1	465.1	74.9	465.1	465.1
1|6|30 Z=F	0.3	465.4	465.4	0.3	465.4	465.4
1|7|10 Batt Voltage	7.6	473.0	473.0	7.6	473.0	473.0
1|8|92 If time is	0.3	473.3	473.3	0.3	473.3	473.3
Output Flag Set @ 18 for Array 108						
1|9|77 Real Time	0.1	473.4	473.4	1.0	474.3	474.3
Output Data 3 Values						
1|10|70 Sample	0.1	473.5	473.5	1.0	475.3	475.3
Output Data 1 Values						
1|11|71 Average	6.4	479.9	479.9	35.1	510.4	510.4
Output Data 11 Values						
1|12|73 Maximum	14.5	494.4	494.4	23.7	534.1	534.1
Output Data 16 Values						
1|13|74 Minimum	14.5	508.9	508.9	23.7	557.8	557.8
Output Data 16 Values						
1|14|96 Serial Out	2.0	510.9	510.9	2.0	559.8	559.8

Program Table 1 Execution Interval 10.000 Seconds

Table 1 Estimated Total Program Execution Time in msec 510.9 w/Output 559.8

Table 1 Estimated Total Final Storage Locations used per day 1152.0

Estimated Total Final Storage Locations used per day 1152.0

B. 21X Micrologger program for Pass Lake 2000

```
;{21X}
;
*Table 1 Program
 01: 10      Execution Interval (seconds) ;

1: Internal Temperature (P17)
 1: 12      Loc [ TC_ref   ]

2: Thermocouple Temp (SE) (P13)
 1: 8       Reps
 2: 2       15 mV Slow Range
 3: 1       SE Channel
 4: 1       Type T (Copper-Constantan)
 5: 12      Ref Temp (Deg. C) Loc [ TC_ref
]
 6: 1       Loc [ Temp_1   ]
 7: 1.0     Mult
 8: 0.0     Offset

3: Volt (Diff) (P2)
 1: 1       Reps
 2: 2       15 mV Slow Range
 3: 5       DIFF Channel
 4: 9       Loc [ Q16744   ]
 5: 320.51  Mult
 6: 0.0     Offset

4: Volt (Diff) (P2)
 1: 1       Reps
 2: 2       15 mV Slow Range
 3: 6       DIFF Channel
 4: 10      Loc [ Q16747   ]
 5: 331.13  Mult
 6: 0.0     Offset

5: Volt (Diff) (P2)
 1: 1       Reps
 2: 2       15 mV Slow Range
 3: 7       DIFF Channel
 4: 11      Loc [ Q11427   ]
 5: 296.74  Mult
 6: 0.0     Offset

6: Z=F (P30)
 1: 1490    F
 2: 13      Z Loc [ LogID    ]

7: Batt Voltage (P10)
 1: 14      Loc [ Battery   ]

8: If time is (P92)
 1: 0       Minutes into a
 2: 60      Minute Interval
 3: 10      Set Output Flag High

9: Real Time (P77)
 1: 1220    Year,Day,Hour/Minute (midnight
= 2400)

10: Sample (P70)
 1: 1       Reps
 2: 13      Loc [ LogID    ]

11: Average (P71)
 1: 11      Reps
 2: 1       Loc [ Temp_1   ]

12: Maximum (P73)
 1: 8       Reps
 2: 10      Value with Hr-Min
 3: 1       Loc [ Temp_1   ]

13: Minimum (P74)
 1: 8       Reps
 2: 10      Value with Hr-Min
 3: 1       Loc [ Temp_1   ]

14: Serial Out (P96)
 1: 30      SM192/SM716/CSM1

*Table 2 Program
 02: 0.0000    Execution Interval (seconds)

*Table 3 Subroutines

End Program

-Input Locations-
1 Temp_1    1 3 1
2 Temp_2    1 3 1
3 Temp_3    1 3 1
4 Temp_4    9 3 1
5 Temp_5    9 3 1
6 Temp_6    9 3 1
7 Temp_7    9 3 1
8 Temp_8    17 3 1
9 Q16744    5 1 1
10 Q16747   1 1 1
11 Q11427   1 1 1
```

12 TC_ref 1 1 1
13 LogID 1 1 1
14 Battery 1 0 1
15 _____ 0 0 0
16 _____ 0 0 0
17 _____ 0 0 0
18 _____ 0 0 0
19 _____ 0 0 0
20 _____ 0 0 0
21 _____ 0 0 0
22 _____ 0 0 0
23 _____ 0 0 0
24 _____ 0 0 0
25 _____ 0 0 0
26 _____ 0 0 0
27 _____ 0 0 0
28 _____ 0 0 0
-Program Security-
0000
0000
0000

Final Storage Label File for: PASS1.CSI
Date: 5/01/2000
Time: 16:31:12

108 Output_Table 60.00 Min
1 106 L
2 Year_RTM L
3 Day_RTM L
4 Hour_Minute_RTM L
5 LogID L
6 Temp_1_AVG L
7 Temp_2_AVG L
8 Temp_3_AVG L
9 Temp_4_AVG L
10 Temp_5_AVG L
11 Temp_6_AVG L
12 Temp_7_AVG L
13 Temp_8_AVG L
14 Light 1_AVG L
15 Light 2_AVG L
16 Light 3_AVG L
17 Light_4_AVG L

18 Temp_1_Hr_Min_MAX L
19 Temp_2_MAX L
20 Temp_2_Hr_Min_MAX L
21 Temp_3_MAX L
22 Temp_3_Hr_Min_MAX L
23 Temp_4_MAX L
24 Temp_4_Hr_Min_MAX L
25 Temp_5_MAX L
26 Temp_5_Hr_Min_MAX L
27 Temp_6_MAX L
28 Temp_6_Hr_Min_MAX L
29 Temp_7_MAX L
30 Temp_7_Hr_Min_MAX L
31 Temp_8_MAX L
32 Temp_8_Hr_Min_MAX L
33 Temp_1_MIN L
34 Temp_1_Hr_Min_MIN L
35 Temp_2_MIN L
36 Temp_2_Hr_Min_MIN L
37 Temp_3_MIN L
38 Temp_3_Hr_Min_MIN L
39 Temp_4_MIN L
40 Temp_4_Hr_Min_MIN L
41 Temp_5_MIN L
42 Temp_5_Hr_Min_MIN L
43 Temp_6_MIN L
44 Temp_6_Hr_Min_MIN L
45 Temp_7_MIN L
46 Temp_7_Hr_Min_MIN L
47 Temp_8_MIN L
48 Temp_8_Hr_Min_MIN L

Estimated Total Final Storage Locations used per day 455.0

Program Trace Information File for:
PASS1.CSI
Date: 5/01/2000
Time: 16:31:12

T = Program Table Number
N = Sequential Program Instruction Location Number
Instruction = Instruction Number and Name

Inst ExTm = Individual Instruction Execution Time
Block ExTm = Cumulative Execution Time for program block,
i.e., subroutine
Prog ExTm = Cumulative Total Program Execution Time

Output Flag High

```
                                Inst Block  Prog
Inst Block  Prog
                                ExTm  ExTm  ExTm
ExTm  ExTm  ExTm
T|N|Instruction                 (msec) (msec)
(msec)  (msec) (msec) (msec)
---------------                 ------ ------ ------  ----
-- ------ ------
1|1|17 Internal Temperature      14.0  14.0
14.0   14.0  14.0  14.0
1|2|13 Thermocouple Temp (SE)    226.4
240.4  240.4   226.4  240.4  240.4
1|3|2 Volt (Diff)               74.9  315.3  315.3
74.9  315.3  315.3
1|4|2 Volt (Diff)               74.9  390.2  390.2
74.9  390.2  390.2
1|5|2 Volt (Diff)               74.9  465.1  465.1
74.9  465.1  465.1
1|6|30 Z=F                      0.3  465.4  465.4
0.3  465.4  465.4
1|7|10 Batt Voltage             7.6  473.0
473.0    7.6  473.0  473.0
1|8|92 If time is               0.3  473.3  473.3
0.3  473.3  473.3
 Output Flag Set @ 18 for Array 108
1|9|77 Real Time                0.1  473.4
473.4    1.0  474.3  474.3
 Output Data 3 Values
1|10|70 Sample                  0.1  473.5
473.5    1.0  475.3  475.3
 Output Data 1 Values
1|11|71 Average                 6.4  479.9
479.9    35.1  510.4  510.4
 Output Data 11 Values
1|12|73 Maximum                 14.5  494.4
494.4    23.7  534.1  534.1
 Output Data 16 Values
1|13|74 Minimum                 14.5  508.9
508.9    23.7  557.8  557.8
 Output Data 16 Values
1|14|96 Serial Out              2.0  510.9
510.9    2.0  559.8  559.8

Program Table 1 Execution Interval  10.000
Seconds

Table 1 Estimated Total Program Execution
Time in msec  510.9 w/Output  559.8

Table 1 Estimated Total Final Storage
Locations used per day 455.0
```

C. 21X Micrologger program for North Willow 2001

```
;{21X}
;
*Table 1 Program
 01: 10      Execution Interval (seconds) ;

1: Internal Temperature (P17)
 1: 12      Loc [ TC_ref   ]

2: Thermocouple Temp (SE) (P13)
 1: 8       Reps
 2: 2       15 mV Slow Range
 3: 1       SE Channel
 4: 1       Type T (Copper-Constantan)
 5: 12      Ref Temp (Deg. C) Loc [ TC_ref
]
 6: 1       Loc [ Temp_1   ]
 7: 1.0     Mult
 8: 0.0     Offset

3: Volt (Diff) (P2)
 1: 1       Reps
 2: 2       15 mV Slow Range
 3: 5       DIFF Channel
 4: 9       Loc [ Q16744   ]
 5: 320.51  Mult
 6: 0.0     Offset

4: Volt (Diff) (P2)
 1: 1       Reps
 2: 2       15 mV Slow Range
 3: 6       DIFF Channel
 4: 10      Loc [ Q16747   ]
 5: 331.13  Mult
 6: 0.0     Offset

5: Volt (Diff) (P2)
 1: 1       Reps
 2: 2       15 mV Slow Range
 3: 7       DIFF Channel
 4: 11      Loc [ Q11427   ]
 5: 296.74  Mult
 6: 0.0     Offset

6: Z=F (P30)
 1: 1490    F
 2: 13      Z Loc [ LogID    ]

7: Batt Voltage (P10)
 1: 14      Loc [ Battery  ]

8: If time is (P92)
 1: 0       Minutes into a
 2: 60      Minute Interval
 3: 10      Set Output Flag High

9: Real Time (P77)
 1: 1220    Year,Day,Hour/Minute (midnight
= 2400)

10: Sample (P70)
 1: 1       Reps
 2: 13      Loc [ LogID    ]

11: Average (P71)
 1: 11      Reps
 2: 1       Loc [ Temp_1   ]

12: Maximum (P73)
 1: 8       Reps
 2: 10      Value with Hr-Min
 3: 1       Loc [ Temp_1   ]

13: Minimum (P74)
 1: 8       Reps
 2: 10      Value with Hr-Min
 3: 1       Loc [ Temp_1   ]

14: Serial Out (P96)
 1: 30      SM192/SM716/CSM1

*Table 2 Program
 02: 0.0000    Execution Interval (seconds)

*Table 3 Subroutines

End Program

-Input Locations-
1 Temp_1    1 3 1
2 Temp_2    1 3 1
3 Temp_3    1 3 1
4 Temp_4    9 3 1
5 Temp_5    9 3 1
6 Temp_6    9 3 1
7 Temp_7    9 3 1
8 Temp_8    17 3 1
9 Q16744    5 1 1
10 Q16747   1 1 1
11 Q11427   1 1 1
```

12 TC_ref 1 1 1
13 LogID 1 1 1
14 Battery 1 0 1
15 _____ 0 0 0
16 _____ 0 0 0
17 _____ 0 0 0
18 _____ 0 0 0
19 _____ 0 0 0
20 _____ 0 0 0
21 _____ 0 0 0
22 _____ 0 0 0
23 _____ 0 0 0
24 _____ 0 0 0
25 _____ 0 0 0
26 _____ 0 0 0
27 _____ 0 0 0
28 _____ 0 0 0
-Program Security-
0000
0000
0000

Final Storage Label File for:
WILLOW01.CSI
Date: 4/23/2001
Time: 10:52:13

108 Output_Table 60.00 Min
1 108 L
2 Year_RTM L
3 Day_RTM L
4 Hour_Minute_RTM L
5 LogID L
6 Temp_1_AVG L
7 Temp_2_AVG L
8 Temp_3_AVG L
9 Temp_4_AVG L
10 Temp_5_AVG L
11 Temp_6_AVG L
12 Temp_7_AVG L
13 Temp_8_AVG L
14 Q16744_AVG L
15 Q16747_AVG L
16 Q11427_AVG L
17 Temp_1_MAX L
18 Temp_1_Hr_Min_MAX L
19 Temp_2_MAX L
20 Temp_2_Hr_Min_MAX L
21 Temp_3_MAX L
22 Temp_3_Hr_Min_MAX L
23 Temp_4_MAX L
24 Temp_4_Hr_Min_MAX L
25 Temp_5_MAX L
26 Temp_5_Hr_Min_MAX L
27 Temp_6_MAX L
28 Temp_6_Hr_Min_MAX L
29 Temp_7_MAX L
30 Temp_7_Hr_Min_MAX L
31 Temp_8_MAX L
32 Temp_8_Hr_Min_MAX L
33 Temp_1_MIN L
34 Temp_1_Hr_Min_MIN L
35 Temp_2_MIN L
36 Temp_2_Hr_Min_MIN L
37 Temp_3_MIN L
38 Temp_3_Hr_Min_MIN L
39 Temp_4_MIN L
40 Temp_4_Hr_Min_MIN L
41 Temp_5_MIN L
42 Temp_5_Hr_Min_MIN L
43 Temp_6_MIN L
44 Temp_6_Hr_Min_MIN L
45 Temp_7_MIN L
46 Temp_7_Hr_Min_MIN L
47 Temp_8_MIN L
48 Temp_8_Hr_Min_MIN L

Estimated Total Final Storage Locations used per day 1152.0

Program Trace Information File for:
WILLOW01.CSI
Date: 4/23/2001
Time: 10:52:13

T = Program Table Number
N = Sequential Program Instruction Location Number
Instruction = Instruction Number and Name

Inst ExTm = Individual Instruction Execution Time
Block ExTm = Cumulative Execution Time for program block,
i.e., subroutine
Prog ExTm = Cumulative Total Program Execution Time

Output Flag High

```
                    Inst Block Prog
Inst Block Prog
                    ExTm ExTm ExTm
ExTm ExTm ExTm
T|N|Instruction          (msec) (msec)
(msec) (msec) (msec) (msec)
-------------           ------ ------ ------ ----
-- ------ ------
1|1|17 Internal Temperature     14.0 14.0
14.0 14.0 14.0 14.0
1|2|13 Thermocouple Temp (SE)  226.4
240.4 240.4 226.4 240.4 240.4
1|3|2 Volt (Diff)          74.9 315.3 315.3
74.9 315.3 315.3
1|4|2 Volt (Diff)          74.9 390.2 390.2
74.9 390.2 390.2
1|5|2 Volt (Diff)          74.9 465.1 465.1
74.9 465.1 465.1
1|6|30 Z=F                 0.3 465.4 465.4
0.3 465.4 465.4
1|7|10 Batt Voltage          7.6 473.0
473.0 7.6 473.0 473.0
1|8|92 If time is          0.3 473.3 473.3
0.3 473.3 473.3
 Output Flag Set @ 18 for Array 108
1|9|77 Real Time           0.1 473.4
473.4 1.0 474.3 474.3
 Output Data 3 Values
1|10|70 Sample             0.1 473.5
473.5 1.0 475.3 475.3
 Output Data 1 Values
1|11|71 Average            6.4 479.9
479.9 35.1 510.4 510.4
 Output Data 11 Values
1|12|73 Maximum            14.5 494.4
494.4 23.7 534.1 534.1
 Output Data 16 Values
1|13|74 Minimum            14.5 508.9
508.9 23.7 557.8 557.8
 Output Data 16 Values
1|14|96 Serial Out         2.0 510.9
510.9 2.0 559.8 559.8

Program Table 1 Execution Interval 10.000
Seconds

Table 1 Estimated Total Program Execution
Time in msec 510.9 w/Output 559.8

Table 1 Estimated Total Final Storage
Locations used per day 1152.0


Estimated Total Final Storage Locations used
per day 1152.0
```

D. Quantum Sensor Calibration Details

Table 1 Calibration identification.

LI-190 Calibration: November 3, 2000	BC Ministry of Forests Research Branch: Peter Fielder (250 356-9549)	LI-1800-02. Optical Radiation Calibrator	Lamp level: 206 □mol.m-2 s-1 (single point calibration)	LICOR lamp :1000 □mol.m-2 s-1

Table 2 Sensors and calibration coefficients (mV/1000)

	Cal. Coeff (mV/1000)			
Sensor	92/93	Nov. 2000	% chng	% chng/yr
Q09684	277.7901	319.3552	13.01532	1.626915
Q11427	323.9979	377.269	14.1202	1.765025
Q10534	322.7347	363.2589	11.15573	1.394466
Q16747	335.8274	354.3235	5.220123	0.745732
Q16744	331.7894	355.4302	6.651324	0.950189
Q16883	359.9194	402.5359	10.58702	1.512431

Table 3. Date, sensor identification, and calibration details for quantum sensors.

	cal				µA			Calconst (µA/1000)		Cal. Coeff (mV/1000)		
Date	code	SN	sa/sb	LAMP	dirty	clned	% DIFF	dirty	clned	dirty	clned	Comment
03-Nov-00	LCM	Q09684	SZ	206.2	1.058	1.069	1.0	5.13	5.18	322.68	319.36	a bit variable
03-Nov-00	LCM	Q11427	SZ	206.2	0.885	0.9049	2.2	4.29	4.39	385.75	377.27	cable chewed
03-Nov-00	LCM	Q10534	SZ	206.2	0.8987	0.9398	4.4	4.36	4.56	379.87	363.26	scratch diffuser
03-Nov-00	LCM	Q16747	SZ	206.2	0.958	0.9635	0.6	4.65	4.67	356.36	354.32	a bit variable
03-Nov-00	LCM	Q16744	SZ	206.2	0.9445	0.9605	1.7	4.58	4.66	361.45	355.43	decreasing signal, I.e., by about 1%
03-Nov-00	LCM	Q16883	SZ	206.2	0.8472	0.8481	0.1	4.11	4.11	402.96	402.54	slow to stabilize, decr.
02-Dec-92	LC	Q09684	SZ	LICOR					5.96		277.79	
02-Dec-92	LC	Q11427	SZ	LICOR					5.11		324.00	
02-Dec-92	LC	Q10534	SZ	LICOR					5.13		322.73	
18-Jan-93	LC	Q16747	SZ	LICOR					4.93		335.83	
18-Jan-93	LC	Q16744	SZ	LICOR					4.99		331.79	
18-Jan-93	LC	Q16883	SZ	LICOR					4.6		359.92	

APPENDIX II

Equipment details and considerations

A. LI-1800 Portable Spectroradiometer

The portable spectroradiometer was implemented to sample light quality. Light quality refers to how light is distributed with respect to wavelength. Some light sources, such as a laser, have a narrow distribution while other sources, such as outdoor sunlight, have a wide distribution. The machine measures the spectral concentration of radiant power by first dispersing the radiation with a diffraction grating monochromater, and measures the energy in each narrow waveband of the resulting spectrum with a silicon detector (Anonymous 1989). Output is shown in $WM^{-2}nm^{-1}$.

The LI-1800 portable spectroradiometer is a battery-operated, microprocessor-controlled spectroradiometer for collecting of spectroradiometric, radiometric and photometric data. The standard optical receptor of the LI-1800 is a PTFE-dome cosine receptor with a 180o (2π steridian) field of view (Anonymous 1989). Scan limits used on all measurements were 300 to 1100nm, with a scan interval of 2nm.

B. Ceptometer

The AccuPAR ceptometer was used to measure light interception in the samples at Sinclair mills. The model PAR-80 was used and consisted of an integrated microprocessor-drive datalogger and probe. The probe itself contains 80 independent photodiodes, spaced 1cm apart (Anonymous 2001). The photodiodes measure PAR (Photsynthetically Active Radiation) in the 400-700nm waveband. The units are displayed in micomols per meter spared per second ($\mu molm^{-2s-1}$). The instrument also allows output as a measure of leaf area index, however only PAR measurements were used in this study.

The manual PAR, full probe, point sample mode, option was used for all measurements taken. Measurements were taken mainly on uniform, overcast. To account for variation in overcast

conditions, two ceptometers were used to take measurements simultaneously in the open and at the sample tree. The results were then presented as a percentage of full light.

C. LAI-2000 Plant Canopy Analyzer

The LAI is an estimate of the amount of foliage in a vegetative canopy by deducing from the measurements how quickly radiation is attenuated as it passes through the canopy. The attenuation is measured at several angles from the zenith, and foliage orientation information is obtained by the instruments. Five zenith angles are measured by the machine simultaneously. The output given is an index of foliage, as it measures all light-blocking objects. The units of LAI are dimensionless, but are thought of as; m^2 foliage area/ m^2 ground area (Anonymous 1992).

The assumptions that must be me for the calculations of foliage amount and orientation to be accurate the following assumptions should be met:

1. The foliage is black. Below-canopy readings do not include any radiation that has been reflected or transmitted by foliage.
2. The foliage is randomly distributed. Foliage containing envelopes must be parallel tubes such as row corps or ingle ellipsoid brush, or infinite box such as turf grass, or deciduous forest.
3. The foliage elements are small compared to the area of view of each ring. The Distance of the sensor to the nearest leaf over it should be at least four times the leaf width.
4. The foliage is azimuthally randomly oriented. The incline of the foliage does not matter as long as all the leaves are not facing in the same compass direction. The importance of this assumption is reduced when a narrow view cap is used or when measurements are made in a wide range of directions. (Anonymous 1992). For all measurements taken with the LAI-2000 plant canopy analyzer the one sensor mode was used. One reading was taken above canopy and four below for each transmittance. A partial covering view cap was used in bright sunlight.

Haiku for the weevil

The little weevil
Looked up to the spruce leader
And climbed to the top